

THE EFFECT OF LAND USE ON GREENHOUSE GAS EMISSIONS ALONG
SALINITY GRADIENTS IN PACIFIC NORTHWEST COASTAL WETLANDS

by

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THESIS ABSTRACT

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Title: The Effect of Land Use on Greenhouse Gas Emissions Along Salinity Gradients in Pacific Northwest Coastal Wetlands

Coastal wetlands can sequester carbon at high rates, but these are offset by the emission of greenhouse gases (GHG). To analyze the effect of land use and environmental predictor variables on GHG emission in coastal wetlands, we measured seasonal in situ trace gas fluxes in 11 restored, 6 reference, and 5 disturbed pasture sites in the Tillamook and Coos Bay, OR. The effects of land use on GHG emissions could be largely explained by physicochemical variables. Pastures had greater CO₂ emissions and lower CH₄ emissions. The restored marshes had lower CO₂ emissions overall and higher CH₄ emissions in Tillamook. Methane emissions were partially controlled by salinity, with methanogenesis almost completely inhibited when salinity > 18 ppt. Nitrous oxide (N₂O) emissions were sporadic and irregular. Our results indicate that restoration of mesohaline and freshwater coastal wetlands may enhance methane emissions, which may offset any positive climate benefits of soil carbon sequestration.

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CHAPTER I

INTRODUCTION

Coastal Wetland Ecosystems

Coastal wetlands are diverse ecosystems that provide habitat and shelter for fish, marine mammals, and shorebirds (Dahl and Stedman 2013; Batzer and Sharitz 2014; Mitsch and Gosselink 2015). These wetlands contribute economic benefits such as providing spawning habitat for commercial fisheries (Dahl and Stedman 2013; Batzer and Sharitz 2014; Mitsch and Gosselink 2015). Additionally, coastal wetlands provide key ecosystem services, such as nutrient removal, carbon sequestration, sediment burial, flood control, and protection against erosion (Chapin and others 2011; Dahl and Stedman 2013; Mitsch and Gosselink 2015). Coastal wetlands are highly dependent on the hydrologic influence from the tides and upland ecosystems. Oceanic influence is greatest in salt water wetlands, where the regular inundation and supply of saline sea water dramatically effects the distribution of local fauna, flora, and supply of nutrients to the ecosystem (Dahl and Stedman 2013; Batzer and Sharitz 2014; Mitsch and Gosselink 2015). While oceanic influence decreases with distance from the ocean (Dahl and Stedman 2013; Batzer and Sharitz 2014), precipitation, snow melt, and ground water sources of freshwater, transport organic matter and nutrients to the hydric soils of downstream reaches (Batzer and Sharitz 2014), further diluting the effects of salinity.

Blue Carbon

Coastal estuaries receive hydrologic inputs from the ocean and rivers, which can contain carbon and nitrogen particulates derived from exogenous sources (Reddy and DeLaune 2008; Harley and others 2015; Mitsch and Gosselink 2015). Alternatively, carbon can be

derived from within the ecosystem, in the form of degrading plant matter (Reddy and DeLaune 2008; Mitsch and Gosselink 2015). Wetlands can act as carbon sinks, in which carbon substances are broken down and stored in the soil or long-lived biomass (Poffenbarger and others 2011). Given the high productivity associated with these ecosystems and the high sediment deposition, coastal wetlands can sequester carbon at highest rate of any ecosystem (Moseman-Valtierra and others 2011). Regular inundation creates an anaerobic environment, which promotes slow microbial decomposition, potentially creating large pools of soil carbon (Chapin and others 2011; Greiner and others 2013). Although coastal wetlands can sequester carbon at one of the highest rates of any ecosystem, this can be offset by emissions of the potent greenhouse gases methane (CH_4) and nitrous oxide (N_2O). While wetlands can sequester carbon at a high rate (Chapin and others 2011; Moseman-Valtierra and others 2011), when wetlands are drained, the aerobic environment promotes subsidence and the oxidation of organic carbon (Chapin and others 2011). Sediment accretion rates in Coos Bay and Siletz Bay (about 50 miles south of Tillamook Bay) are ~ 3.3 mm/yr (Thorne and others 2018), which currently exceeds the rate of sea level rise of 0.0426 mm/yr in Northern California (Komar and others 2011) and - 0.003 to -0.004 mm/yr in Northern Oregon, although there is large variation among studies and locations along the coast (Montillet and others 2018). Due to the high rate of carbon sequestration, coastal wetlands have attracted a lot of attention as a potential to mitigate the effects of global climate change (Murdiyarso and others 2015). Given the large variability of sea level rise and sediment accretion, it is of the upmost interest in to more finely characterize carbon dynamics of coastal wetlands in the Pacific Northwest.

Coastal Wetlands and Degradation

Coastal wetlands are susceptible to anthropogenic forces and their degradation can be linked to the density of human populations along the coastlines, which are typically accompanied by the anthropologic development and drainage of wetlands, changes in hydrology, and habitat fragmentation (Stedman and Dahl 2008; Mitsch and Gosselink 2015). In the continental United States, it is estimated that the total area of coastal wetlands decreased by 146,000 from 2004 to 2009, which is 1.25 times greater than rates reported from 1998 to 2004 (Dahl and Stedman 2013). Saltwater wetlands were estimated to have declined by 38,000 ha and freshwater wetlands declined by 107,000 ha, although the Pacific coastal region recorded minor losses in comparison to the Atlantic and Gulf of Mexico (Dahl and Stedman 2013). Pacific coastal wetlands are estimated to have decreased by about 2,000 ha from 2004 to 2009 (Dahl and Stedman 2013).

Wetland Policy

Following the instatement of the No Net Loss policy in 1988, the United States has made it a goal to retain and/or increase the total acreage of wetlands in an attempt to conserve this vital ecological resource (Bendor 2009). This policy aims to retain the cumulative acreage of wetlands, by encouraging wetland restoration to mitigate loss (Bendor 2009).

Global Warming Potential

Even though estuaries demonstrate high rates of carbon sequestration, they can ultimately have a net positive radiative forcing (i.e., a warming effect) (Poffenbarger and others 2011). Estuaries can emit significant amounts of the potent GHGs CH₄ and N₂O, which can offset high carbon sequestration rates (Barnes and Upstill-Goddard 2011;

Borges and Abril 2011). Given a 100-year time scale and sustained emissions, CH₄ has 45 times the global warming potential as carbon dioxide (CO₂) and N₂O has 263 times the global warming potential (Neubauer and Megonigal 2015). Thus, CH₄ and N₂O emissions should be converted to CO₂ equivalents in order to evaluate variation in GHG emissions.

Carbon Dioxide Emissions

In this study, we focus on ecosystem respiration, which accounts for microbial heterotrophic respiration and plant respiration, but not photosynthesis (Reddy and DeLaune 2008; Chapin and others 2011). Plant respiration is greatly influenced by the immediate availability of sunlight, due to the shared products and reactants of photosynthesis, and may limit respiration in its absence (Reddy and DeLaune 2008). This is of particular interest when considering CO₂ emissions, as most studies use dark chambers to estimate GHG fluxes, thus inhibiting photosynthesis.

Estuaries can produce large amounts of CO₂, through bacterial respiration (Borges and Abril 2011). In aerobic respiration, oxygen is utilized as the terminal electron acceptor (Borges and Abril 2011). After prolonged inundation, when oxygen becomes depleted, anaerobic processes utilizing alternative terminal electron acceptors will dominate, but still yield CO₂ (Froelich and others 1979). Alternative terminal electron acceptors are consumed in order of decreasing Gibbs free energy (oxygen > nitrate ~ manganese oxides > iron oxides > humic-reduction > sulfate-reduction) (Froelich and others 1979; Oldham and others 2017). Due to the high input of sulfate in marine systems, methanogens may be out competed by sulfate reducing bacteria, resulting in CO₂ production (DeLaune and others 1983; Poffenbarger and others 2011). In partially

inundated soils, CH₄ diffusing upward in the soil profile can be microbially oxidized via methanotrophy (Hanson and Hanson 1996). In marine systems, the majority of CH₄ produced is oxidized through processes of anaerobic oxidation of methane (AOM), which couples sulfate-reduction to methane-oxidation (Antler and others 2014).

Soil temperature has found to be positively correlated with CO₂ emissions (Reddy and DeLaune 2008; Yamochi and others 2017), while water table height has a negative correlation (Reddy and DeLaune 2008; Yamochi and others 2017). Additionally, CO₂ fluxes have been found to be negatively correlated to salinity (Reddy and DeLaune 2008; Hu and others 2017).

Methane Emissions

Methane is produced primarily under anaerobic conditions, where methanogens use the products of anaerobic fermentation to create metabolic energy, ultimately producing CH₄ (DeLaune and others 1983; Reddy and DeLaune 2008; Chapin and others 2011). In the absence of oxygen, microbes use the next most efficient terminal electron acceptor (Froelich and others 1979; Chapin and others 2011). Methanogenesis is a particularly unfavorable process and methanogens may be outcompeted by microbes that can utilize more favorable terminal electron acceptors. When CH₄ is produced and diffuses upward, it can be oxidized in the aerobic zone of a partially inundated soil (Hanson and Hanson 1996). In the anoxic zone, AOM can consume upward diffusing CH₄ by coupling the reaction with sulfate-reduction (Reddy and DeLaune 2008; Antler and others 2014), manganese-reduction, iron-reduction, or humic-reduction (Froelich and others 1979; Oldham and others 2017)

Methane production is often inversely related to salinity, which is correlated with

the sulfate concentration in the soil (DeLaune and others 1983; Reddy and DeLaune 2008; Poffenbarger and others 2011). This is primarily the product of the inhibition of methanogens due to competition with sulfate-reducing bacteria (DeLaune and others 1983; Reddy and DeLaune 2008). The concentration of pore water sulfate decreases down the soil profile, where it is depleted at the sulfate-methane transition zone (Antler and others 2014). Methane inhibition is dependent on the concentration of sulfate, where concentrations >4 mM have been found to completely inhibit CH_4 production (Poffenbarger and others 2011). This study found that polyhaline marshes emitted the lowest amount of CH_4 , but due to high variability in emissions from freshwater, oligohaline, and mesohaline estuaries, a linear relationship between salinity and CH_4 emission was not found. Moreover, the highest variability was found in freshwater and oligohaline estuaries. The authors suggest that the high variability in CH_4 emission could be due to irregular supply of diffusing sulfate and variable rates of methane-oxidation (Poffenbarger and others 2011). Sulfate may be limited within the soil profile through inadequate diffusion of oceanic water or may create zones/ microsites of high sulfate-reduction, inferring that salinity might not accurately reflect sulfate concentration (Poffenbarger and others 2011). Antler et al. (2014) found that the mechanisms of sulfate-reduction and regeneration varied among sites in the Mediterranean coast of Israel. Sulfate was exclusively depleted through AOM in the Yarkon estuary, while both AOM and bacterial sulfate-reduction accounted for the sulfate depletion in the Qishon estuary. Methanogens are at a competitive disadvantage when in the presence of O_2 , NO_3^- , Fe^{3+} , and sulfate, but these substrates are generally sparse in freshwater soils, which may create spatial variation in their availability (Poffenbarger and others 2011).

In addition, CH₄ emissions have been found to be positively correlated to temperature, while displaying temporal (monthly and seasonal) and spatial variation (Poffenbarger and others 2011; Harley and others 2015; Hu and others 2017). Thus, the highest CH₄ fluxes often occur in the summer and the lowest in the winter (Harley and others 2015; Hu and others 2017). The increased CH₄ emission during warm months could be linked to increased microbial-mediated organic matter decomposition, which provides carbon for methanogens, or direct increases in methanogen metabolism (Hu and others 2017).

Plant root rhizospheres can mediate transport of CH₄ to the surface through their vascular tissue (Reddy and DeLaune 2008). Additionally, they can create a layer of oxygen around the roots, locally inhibiting methanogenesis (Reddy and DeLaune 2008). When comparing the microbial functional traits associated with mud flats and vegetated marshes dominated by halophyte communities, it was found that there was a higher proportion of methanogens to methanotrophs in halophyte-dominated soil than the mudflat ecosystem (Chaudhary and others 2017). This infers that mudflat ecosystems oxidize more CH₄ produced than halophyte dominated estuaries. Furthermore, mudflat ecosystems were found to contain fewer sulfate-reducing bacteria compared to methanogens than halophytic communities (Chaudhary and others 2017). Additionally, halophytic plant communities demonstrated higher extracellular enzyme activity, which is the product of the microbial communities associated with the halophytic root systems (Chaudhary and others 2017). Therefore, plant communities can have implications on the composition of soil microbial communities responsible for CH₄ production and consumption, as well as sulfate-reduction.

Nitrous Oxide Emissions

Nitrous oxide is primarily emitted from estuarine soils through microbial processes of denitrification, in which NO_3^- is reduced to form N_2 , and nitrification, which oxidizes NH_4^+ to form NO_3^- (Chapin and others 2011). Denitrification is heterotrophic, while nitrification is mediated by autotrophic bacteria (Barnes and Upstill-Goddard 2011). The production of N_2O is dependent on the degree of nutrient loading and availability of NO_3^- or NH_4^+ as substrates for nitrification or denitrification (Harley and others 2015). The production of N_2O has been found to vary substantially along spatial gradients (Barnes and Upstill-Goddard 2011; Harley and others 2015). Barnes and Upstill-Goddard (2011) found that within European estuaries, low salinity estuaries produced the greatest amounts of N_2O . Harley et al. (2015) found CO_2 and N_2O saturation to be positively correlated, resulting from either shared environmental controls between CO_2 production and denitrification, and/or CO_2 production via denitrification.

Generally, N_2O emissions are positively correlated with temperature, but this trend is not always the case (Barnes and Upstill-Goddard 2011). Nitrous oxide emissions demonstrate temporal variation, where the highest emissions occur in the summer and lowest in the winter (Barnes and Upstill-Goddard 2011; Harley and others 2015), although other studies reported peak N_2O concentrations in the wet season (Nirmal Rajkumar and others 2008). Additionally, anthropogenic pollution by means of agricultural runoff of nitrogen containing fertilizers like urea and ammonium phosphate can affect GHG emissions (Nirmal Rajkumar and others 2008).

Wetland Restoration

Given the importance of coastal wetland ecosystems and their potential to mitigate global GHG emissions, there is a lot of interest in restoring these ecosystems (Murdiyarso and others 2015). There is interest in utilizing their carbon sequestration capacity as a way of funding restoration with associated carbon credits, potentially mitigating global carbon emissions (Shiau and others 2019). Additionally, saline and brackish marshes have been highlighted for their potential to emit low levels of CH₄ relative to fresh wetlands (Shiau and others 2019). Passive restoration acts to restore hydrologic influence by removing dikes and tidal gates (Cornu and Sadro 2002). If there is substantial subsidence, active restoration practices may be applied to alter the wetland surface elevation (Cornu and Sadro 2002), manipulating stream morphology, and/or removing invasive plant species and planting native wetland species (Cornu 2005a). In Quebec Canada, agricultural fields passively restored salt marshes, by returning tidal flow via dike removal were found to emit less CO₂ following restoration, although this commodity may be lost as the marsh ages (Wollenberg and others 2018). Additionally, both natural and passively restored marshes were found to act as net sources of CH₄ and N₂O, following dike removal (Adams and others 2012). Natural sites were found to emit relatively large amounts of CH₄ and low amounts of N₂O, when compared to passively restored sites (Adams and others 2012).

Research Context

To my knowledge, my research is the first to examine trace gas fluxes in Oregon estuarine wetlands, and some of the first in the Pacific Northwest. Estuaries in California and on the East and Gulf Coasts of the U.S. have been the subject of extensive prior

research on trace gas emissions, but Pacific Northwest estuaries vary from these other U.S. estuaries in substantial ways that would be expected to affect trace gas fluxes, e.g., climate and dominant plant communities. Moreover, there has been very little research done on GHG emissions in restored wetlands, and this has been identified as a major priority (Bridgham and others 2006). The experimental design allowed for the comparison of land uses and the effect of salinity on coastal estuaries in the Pacific Northwest, Coos Bay and Tillamook. This research is important for the conservation of estuaries because Oregon has an extensive history of diking and draining their coastal wetlands for agricultural land uses. Recently, many of these drained fields have been restored but it is currently unknown how different restoration practices compare in regard to GHG production.

CHAPTER II

THE EFFECT OF LAND USE ON GREENHOUSE GAS EMISSIONS ALONG SALINITY GRADIENTS IN PACIFIC NORTHWEST COASTAL WETLANDS

Introduction

Coastal wetland ecosystems receive both freshwater and saline seawater inputs from the ocean and riverine systems, creating salinity gradients (Dahl and Stedman 2013; Mitsch and Gosselink 2015). Estuaries provide habitat for various flora and fauna, as well as remove nutrients, sequester carbon, and protect against erosion and flooding (Dahl and Stedman 2013; Mitsch and Gosselink 2015). They have the highest soil carbon sequestration rates per area of any ecosystem type (Mcleod and others 2011; Moseman-Valtierra and others 2011).

In the continental United States, increases in the human population along the coast lines have led to the development and drainage of coastal wetlands (Dahl and Stedman 2013). Saltwater wetlands have declined by 38,000 ha and freshwater wetlands have declined by 107,000 ha from 2004 to 2009, although the majority of loss occurred on the Atlantic coast and Gulf of Mexico (Dahl and Stedman 2013). Pacific coastal wetlands experienced a reduction of about 2,000 ha, although their limited distribution had already been heavily impacted by 2004 (Dahl and Stedman 2013).

There is increasing interest in utilizing their carbon sequestration capacity as a rationale for their restoration, including the potential use of carbon credits as a funding mechanism (Shiau and others 2019). The high rate of soil carbon sequestration by estuarine wetlands is partially offset by their emission of greenhouse gases (GHG) such as methane (CH_4) and nitrous oxide (N_2O) (Barnes and Upstill-Goddard 2011; Borges

and Abril 2011; Neubauer and Megonigal 2015), potentially giving them a net positive radiative forcing effect (i.e., a warming effect) (Poffenbarger and others 2011). Given a 100-year time scale and sustained emissions, CH₄ has 45 times a sustained-flux global warming potential as carbon dioxide (CO₂) and N₂O has 263 times the global warming (Neubauer and Megonigal 2015).

Methane is produced in anaerobic conditions, when other terminal electron acceptors are depleted (Reddy and DeLaune 2008; Chapin and others 2011). Methane emissions are often inversely correlated with salinity (DeLaune and others 1983; Reddy and DeLaune 2008; Poffenbarger and others 2011) and sulfate concentration due to competition with sulfate-reducing bacteria (DeLaune and others 1983; Reddy and DeLaune 2008; Chapin and others 2011). Freshwater, oligohaline, and mesohaline marshes can emit large amounts of CH₄, but have displayed high variability, making it difficult to classify them as net sources or sinks (Poffenbarger and others 2011).

Nitrous oxide is produced in coastal wetland soils through microbial processes of denitrification, where NO₃⁻ is reduced to N₂, and nitrification, which oxidizes NH₄⁺ to NO₃⁻ (Harley and others 2015). Nitrous oxide emissions in wetlands are often low but can be high with high nutrient loading (Adams and others 2012; Wollenberg and others 2018), e.g., in wetlands restored from former farm fields. This implies that waters polluted by agricultural runoff can lead to increased GHG production, potentially turning GHG sinks into net sources.

There is much interest in restoring estuaries for their potential to mitigate global GHG emissions (Murdiyarso and others 2015). In Quebec Canada, both natural and passively restored salt marshes were found to act as net sources of CH₄ and N₂O, following the

removal of the dikes (Adams and others 2012). Natural sites were found to emit relatively large amounts of CH₄ and low amounts of N₂O, when compared to passively restored sites, and suggest that disturbed sites may sequester high amounts of CO₂, but act as net sources of CH₄ and N₂O immediately after reintroduction of tidal flow (Adams and others 2012). Little is known about the influence of wetland disturbances and restoration on trace gas emissions, which could be drastically different in the Pacific Northwest. Due to the high variation in CO₂ (Harley and others 2015; Hu and others 2017), CH₄ (Poffenbarger and others 2011), and N₂O emissions (Barnes and Upstill-Goddard 2011; Harley and others 2015), it is important to understand the local controls on GHG emissions to inform restoration design and practices. Additionally, while the relationship between CH₄ and sulfate are well studied in marine environments, there is a lot of variability between studies and locations, inferring that there are additional factors influencing CH₄ emissions other than sulfate concentration, which may be apparent when analyzed along a salinity gradient. In this study we addressed the following questions: What is the influence of environmental controls on GHG emissions in Pacific Northwest coastal wetlands? How do trace gas emissions in Pacific Northwest coastal wetlands vary along salinity gradients? How are GHG emissions in Pacific Northwest coastal wetlands influenced by changes in land use?

Methods

Site Description

In order to evaluate the effects of land use in Pacific Northwest estuaries, GHG fluxes were measured in 22 total sites that varied in land use (reference, disturbed, or restored) and in salinity along the Oregon Coast in Tillamook Bay and Coos Bay.

Coos Bay Sites. Coos Bay (Figure 1) is located along the southern coast of Oregon and is most notably developed by the coastal towns Coos Bay and North Bend (combined population = 25,662) (US Census Bureau 2010). It has a moderate Mediterranean climate with warm, dry summers and cool, wet winters, with a mean annual temperature of 11.5 °C and mean annual precipitation of 163.6 cm (US Climate Data 2019) The sites in Coos Bay were subdivided into salinity classes (polyhaline (13-35 ppt), mesohaline (3-35 ppt), and fresh (0-2 ppt), corresponding to the natural salinity gradient from the bay to the upper reaches of the South Slough.

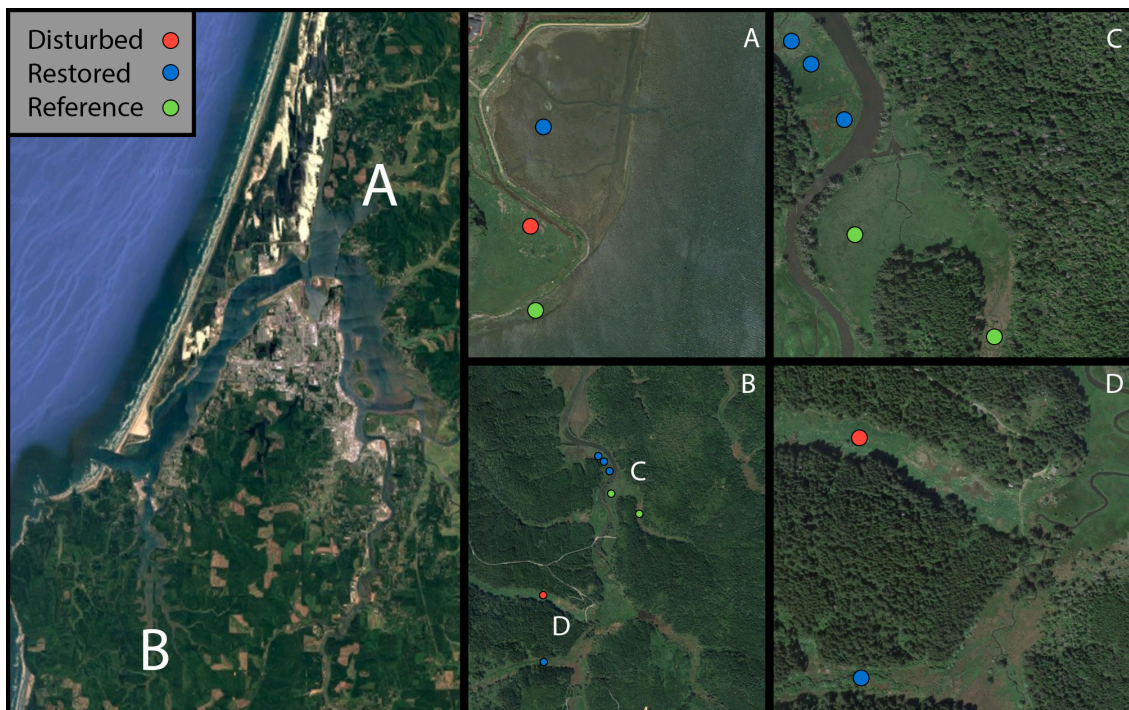


Figure 1. Google maps images of Coos Bay sites. On the left is the Coos Bay. A depicts the salt marsh complex. B depicts the South Slough. C portrays the location of the Kunz marsh restoration and Tom's creek reference mesohaline and freshwater sites. D indicates the location of disturbed site Wasson creek and restored freshwater site Anderson creek.

The salt marsh complex (Figure 1A) is along the northern end of the Coos Bay (Figure 1) and is owned by a private land owner. In 1934, this marsh was diked and converted to agriculture, except for a narrow band of remnant marsh along the bay (our

reference salt marsh site). This reference site is dominated by *Salicornia sp.* and is regularly inundated. In 2003, the dike was removed in about one-third of the site, returning tidal flow and creating a mudflat with no vascular vegetation except for scattered *Zostera zaponica* (our restored salt marsh site). Part of the site remains diked and ditched and is currently grazed by cattle (our disturbed salt marsh site). The restored and reference marshes have salinity of about 25-33 ppt, while the disturbed field has a salinity of 0-23 ppt, due to winter and spring precipitation diluting the effects of salinity that bleed through the surrounding dikes. The influence of salinity in the pasture was highest near the dike border the bay, although high precipitation created a fresh (0-1 ppt) environment much of the winter and spring.

Our mesohaline and freshwater wetland sites are located in the South Slough National Estuary Reserve at the southern end of the Coos Bay (Figure 1). Kunz marsh (5 ha) is a mesohaline site that prior to restoration in 1996 had been drained and used for agriculture in the early 1900s (Cornu and Sadro 2002; Cornu 2005b). To examine the role of initial marsh elevation on restoration trajectories, the marsh was divided into four cells, and separated by 1.8 m tall geotextile cloth. One cell was graded to a high marsh (2.4 m above mean lower low water (MLLW)) (0.53 ha), one to a mid-level marsh (2.0 m above MLLW) (0.56 ha), and two to low marshes (1.7 m above MLLW) (0.54 ha; 0.59 ha). The responses for the first three years in sediment deposition, plant community structure, fish usage, and tidal channel development are reported in Cornu and Sadro (2002). In 2016, the geotextile cloth was removed, but sites still reflect distinct transitions in marsh elevation between cells. Kunz marsh is dominated by *Carex lyngyei*, *Deschampsia caespitosa*, and *Agrostis spp* (Cornu and Sadro 2002; Cornu 2005b). We

observed that the low marsh cells are inundated half of the day, the mid marsh at high tide, and the high marsh is infrequently fully inundated.

Tom's Creek Marsh (Figure 1) differs greatly in salinity, water saturation, and vegetation from east to west. The western side of Tom's Creek Marsh is our mesohaline reference site. It has a salinity of about 5-33 ppt and is dominated by *Agrostis alba*, *Distichlis spicate*, and *Triglochin maritimum* (Cornu and Sadro 2002). This site was diked but never fully converted to agriculture, and has remained tidally influenced for the last 40 years (Cornu and Sadro 2002). Cornu and Sadro (2002) also used it as a reference site in their study, in addition to a nearby site (Danger Creek Marsh) that had never been diked. The two reference sites had similar sedimentation rates and vegetation structure. We have also found the reference sites have similar O soil horizons in terms of depth and organic matter content (unpublished data).

We used the freshwater marsh to the eastern side of Tom's Creek Marsh as our freshwater reference site. It has never been diked and is formed by a meandering stream (Tom's Creek), giving it a water table around the soil surface throughout the year. It has limited tidal influence (< 10 cm) and constant freshwater input with a salinity of 0-1 ppt. It is dominated by trees, shrubs and sedges, such as *Alnus rubra*, *Lysichiton americanus*, and *Carex obnupta*.

Anderson Creek Marsh is a restored freshwater wetland that is just above the tidal influence. Prior to restoration, Anderson Creek Marsh had been drained and used for agriculture since around the turn of the 20th century. Agriculture was abandoned in the 1970s but the down cut ditch and lowered water table remained (Cornu 2005a). The restoration took place in 2002, in which the creek was made much shallower and its sinuosity greatly increased in an attempt to recreate the conditions prior to drainage. The

top 20-60 cm of topsoil was removed to fill the drainage ditch. Additionally, native vegetation was planted (Cornu 2005a). Currently the site is dominated by *Carex obnupta*, *Scirpus microcarpus*, *Myrica californica*, and *Vaccinium ovatum* (Cornu 2005a).

We used Wasson Creek Marsh as a disturbed freshwater site. It is in a parallel drainage just to the north of Anderson Creek Marsh across a ridge, and it has a similar disturbance history except it has never been restored. A road at the lower end of the marsh acts as a dam, so the lower portion of the marsh is relatively wet and dominated by *Phalaris arundinacea* (Turnbull and Bridgham 2015). However, our sampling site in the upper section continues to have a lowered water table more because of an intact ditch and is dominated by non-native grasses and forbs reflective of a relatively dry, abandoned pasture.

Tillamook Bay Sites. Tillamook Bay (Figure 2) is located along the northern Oregon coast, west of Tillamook, OR (population = 4,935)(US Census Bureau 2010). It also has a moderate Mediterranean climate with a mean annual temperature of 10.7 °C and mean annual precipitation of 223.5 cm (US Climate Data 2019). Tillamook is a major dairy producer on the West Coast and many of the wetlands in the county were drained since the early 1990s to accommodate 15,000 ha of farm land (USDA-NASS 2012). On the southern end of the Tillamook Bay, 211 ha of land in the Southern Flow Corridor (SFC) (Figure 2B) was restored in 2015-2016. The restoration removed 11 km of levees, dug new channels, and added large woody debris in an attempt to restore tidal flow, create fish habitat, and decrease flooding in Tillamook (Brown and others 2016). High precipitation and flooding in Tillamook Bay during winter and spring led to large fluctuations in salinity throughout the year.

We established six sites that spanned the restoration and reflected the diverse conditions throughout the SFC (Figure 2B). The northern most site was dominated by *Typha sp.* and had a salinity of 0-5 ppt. The rest of the restoration was heavily dominated by *Phalaris arundinacea* and *Carex obnupta*. The two westmost sites had water tables greater than - 10 cm much of the year and had salinity that ranged 5-27 ppt. The two southern most sites had a salinity of 5-20 ppt and were inundated daily. The middle site had a salinity of 2-20 and was under 0.3 m of water throughout the year.

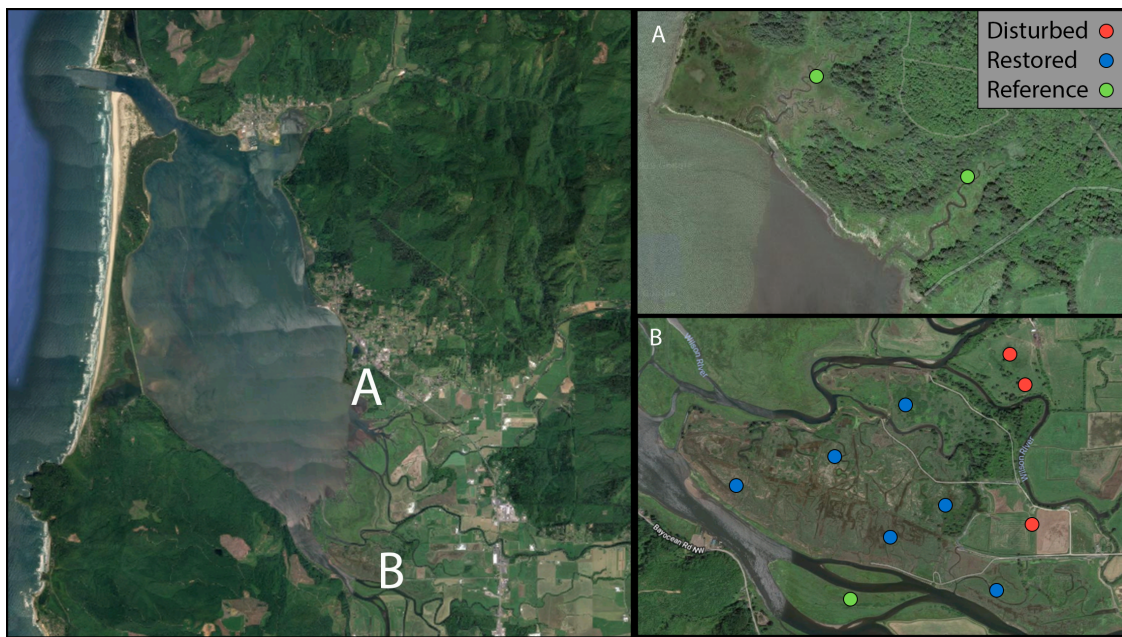


Figure 2. Google maps Images of sites in Tillamook Bay. Image on the left displays the SFC restoration, Dry Stocking Island reference site, and agricultural fields. On the right are the reference sites Goose Point and Doty Creek.

We established three high marsh reference sites with no evidence of agricultural disturbance. Dry Stocking Island (Figure 2B) is located just south of the SFC restoration. It is dominated by *Deschampsia spp.* (tufted hairgrass) and was rarely fully submerged by water. Goose point and Doty Creek marsh are north of the SFC restoration (Figure 2A). They were dominated by *Argentina spp.* (Pacific silverweed), had a salinity that ranged from 5-28, and were regularly inundated.

Bordering the SFC restoration to the northeast are three private agricultural farm fields that served as our disturbed sites. These farms were converted from high marsh to agricultural fields through diking and draining in the early 1900's (C. Allen personal communication 2017; J. Thorne personal communication 2017). These pastures had a water table below - 50 cm throughout the summer and experienced large ponding events periodically throughout the winter. The southernmost disturbed site was part of the original pasture that was divided and sold for the restoration. Due to arrangements with the Tillamook Estuaries Partnership (TEP), additional dikes and tidal gates were installed to reduce flooding in the winter, thus it had a low water table throughout the year. Pasture sites had a salinity of 0 ppt all year.

GHG Flux Measurements

Carbon dioxide, methane, and nitrous oxide were measured in situ with a portable Fourier-transform infrared (FTIR) gas analyzer (Gasmeter DX4040) using dark chambers in a closed-loop configuration. Dark chamber CO₂ emissions measure net ecosystem respiration and included plant and heterotrophic soil respiration. Gas measurements were measured at 10 Hz and averaged every 30 seconds for approximately 10 minutes. Gas fluxes that did not yield a significant change in concentration ($P < 0.05$) after 10 minutes were deemed to be zero. Methods that allow for in situ continuous measurement of gas concentrations are a significant advance over the traditional method of taking a small number of point-gas samples with syringes over long incubation periods in static chambers because they allow for short measurement periods and a high density of sample points to determine the linearity of the response. In order to avoid influencing gas release from the soil, boardwalks were placed at each site with one chamber at each end of the

2.44 m long boardwalk. Two types of chambers made out of PVC were used in this experiment (28.5 cm diameter by 27 cm height and 39.5 cm diameter by 34 cm height). Sampling occurred eight times within one water year (October to September) in Tillamook and six time in Coos Bay to estimate the seasonality and yearly GHG emissions. A floating chamber was crafted by adhering Styrofoam to the exterior of the chamber to sample GHG at high tide. The snapshot high tide sampling was conducted in late September 2019 and measured the sites that had not been sampled at high tide in order to estimate the influence of tides on GHG emissions. In Coos Bay, tidal sites were measured at both high and low tide during the same time frame.

Environmental Variables

At each chamber, soil temperature was taken at 10 cm depth during each sampling period. Shallow (30 cm) and deep (85 cm) well were made out of 3/4" PVC pipes and placed at each boardwalk. Water-table height, porewater salinity and pH were recorded by measuring the height of the water table in the shallow well and then extracting a porewater sample to be analyzed in the field with a refractometer and portable pH analyzer. When the water table was < -30 cm, the deep wells were used for pore water samples.

In September 2018, to assess the correlation between sulfate and salinity, soil pore water was extracted from the wells at each board walk, passed through a 0.7 μm filter, and put on ice before being stored frozen at the University of Oregon. Soil pore water samples were analyzed by the UC Davis analytical lab for sulfate via ion chromatography.

Some the gas flux sites had soil carbon content data already available in both

Tillamook Bay (Peck, 2017) and in Coos Bay (Blount, 2017). Erin Peck took one 50 cm core at six of the sites in Tillamook, split into 2 cm increments, and analyzed for % carbon on an elemental analyzer. Keyanna Blount took five cores from each of the Coos Bay polyhaline and fresh sites, divided them into 0-15 and 15-30 cm increments and analyzed % carbon on an elemental analyzer. Emil Sadofsky extracted six shallow cores (approximately 15 cm) from the four mesohaline sites in Coos Bay and analyzed them for loss-on-ignition (LOI) (unpublished data). All depths within the first 15 cm were averaged to estimate % carbon in the top 15 cm of the soil. Additionally, six 0-15 cm deep replicate soil cores were extracted with PVC cores (5 cm diameter, 15 cm length) during the summer of 2018 from the six remaining Tillamook Bay sites. Cores were placed in a refrigerator at 8° C until sample analysis. Roots were hand-picked and the remaining soil was homogenized, dried for at least 48 hours at 60 °C, and then ground with a pestle and mortar. Samples were then analyzed for % organic matter with LOI in a muffle furnace at 550 °C. LOI was converted to % carbon using a ratio of % carbon to organic matter of 0.5.

Statistical Analysis

Analysis was performed considering Coos Bay and Tillamook Bay both separately and combined using R 3.5.2 statistical package with RStudio 1.1.463. Given the many zero values, CH₄ and N₂O fluxes could not be transformed to approximate a normal distribution, so we used nonparametric statistical techniques throughout. To analyze the contribution of environmental predictor variables on GHG emissions, we used the R packages rpart to create Classification and Regression Trees (CARTs) and rparty to create plots. CARTs were pruned by determining the split that provided substantial increases in model correlation, while reducing the cross-validation error of the

model (James and others 2013). Subsequent Random Forests were generated with the R package randomForest to rank the importance of the environmental predictor variables (James and others 2013). Linear models were generated to assess to correlation between environmental predictor variables and trace gas emissions.

We also examined the effect of land use and environmental variables on gas emissions with Bayesian statistics use the R the package Rstan. Variables were given sparsifying priors with a normal distribution (mean = 0; standard deviation = exponential 1) and put on a common scale with the scale function in R. The statistical significance of land use and influence of environmental variables were evaluated based on 95% credibility intervals of the posteriors, generated after 10,000 (4,000 warmup: 6,000 sampling) random-walk iterations in Rstan.

All models (CARTS, Random Forests, and Bayesian) were cross-validated by training the models on a 1/10 of the data, testing on the remaining 9/10, and comparing the root mean square of the difference between the estimate and the actual data. Final models were used to estimate annual GHG fluxes with the continuously measured environmental data in Tillamook bay. Additionally, GHG measurements were linearly interpolated between observed fluxes in Coos Bay and Tillamook. Final annual emissions were compared between model estimates and linear interpolation in Tillamook, but this was not possible in Coos Bay, as we did not continuously measure environmental predictors.

Results

A. Carbon Dioxide

Combined Sites. CARTs explained 40% percent of the variation in dark CO₂

emissions and revealed that emissions were controlled by water table height, air temperature, soil temperature, and land use (Figure 3). Emissions were greatest when the water table was below -4.5 cm and the air temperature was above 26 °C (mean = 1.0 $\text{mol}^{-2} \text{d}^{-1}$). At temperatures between 10.4 and 26.0 °C, disturbed and reference marshes emitted greater fluxes (mean = 0.53 $\text{mol}^{-2} \text{d}^{-1}$) than restored marshes (mean = 0.23 $\text{mol}^{-2} \text{d}^{-1}$). When soil temperatures were below 10.4 °C or the water-table was higher than 4.5 cm, low CO_2 emissions occurred (mean = 0.23 and 0.13 $\text{mol}^{-2} \text{d}^{-1}$, respectively). The effect of temperatures and land use were evident in the seasonal dynamics of emissions with higher emissions in the summer in Coos Bay and in May in Tillamook Bay and often lower emissions in restored sites in both bays (Supplemental Figure 1).

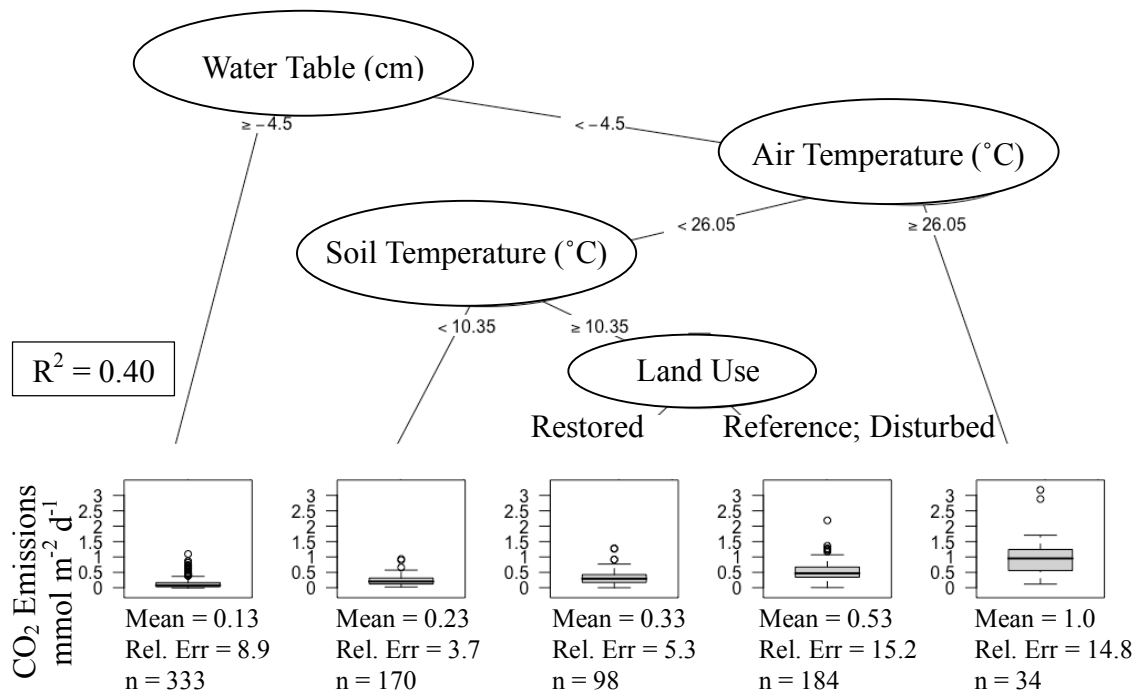


Figure 3. CART results for CO_2 emissions from both Coos Bay and Tillamook Bay sites. Ovals depict model splits with associated P-values. They correspond to terminal leaf boxplots with mean CO_2 emissions, relative error, and number of samples (n). The overall model Psuedo – $R^2 = 0.40$.

Random forests explained 60 % of the variation in CO₂ emissions and emissions were heavily influenced by air temperature and water table ($p < 0.001$, Table 1). Individual regressions, CO₂ emissions were weakly correlated with salinity ($p < 0.001$, $R^2 = 0.03$, Supplemental Figure 2A) water table height ($p < 0.001$, $R^2 = 0.19$, Supplemental Figure 2B) and air temperature ($p < 0.001$, $R^2 = 0.16$, Supplemental Figure 2D). Bayesian models revealed significant differences in land use on observed fluxes, with restored sites having lower emissions than disturbed and reference sites, and restoration decreasing emissions (Table 2).

	CO ₂	Coos Bay CH ₄	N ₂ O	CO ₂	Tillamook CH ₄	N ₂ O	CO ₂	Combined CH ₄	N ₂ O
Water Table	1.00	0.42	0.40	0.79	1.00	0.41	0.94	0.70	0.50
Salinity	0.36	0.52	0.21	0.43	0.73	0.42	0.40	0.67	0.40
Soil Temperature	0.56	1.00	0.50	0.52	0.98	1.00	0.59	1.00	0.89
Air Temperature	0.66	0.85	0.33	1.00	0.85	0.72	1.00	0.80	0.68
pH	0.43	0.59	1.00	0.33	0.89	0.69	0.39	0.67	1.00
% Carbon	0.44	0.65	0.18	0.24	0.43	0.65	0.35	0.57	0.66
Land Use	0.26	0.22	0.09	0.21	0.19	0.12	0.24	0.19	0.21
R-Squared	0.61	0.10	0.01	0.60	0.28	0.04	0.60	0.21	0.03
P-value	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001

Table 1. Random forest model results for GHG emissions in Coos Bay, Tillamook, and PNW datasets. Values indicate relative importance of predictor variables in GHG models.

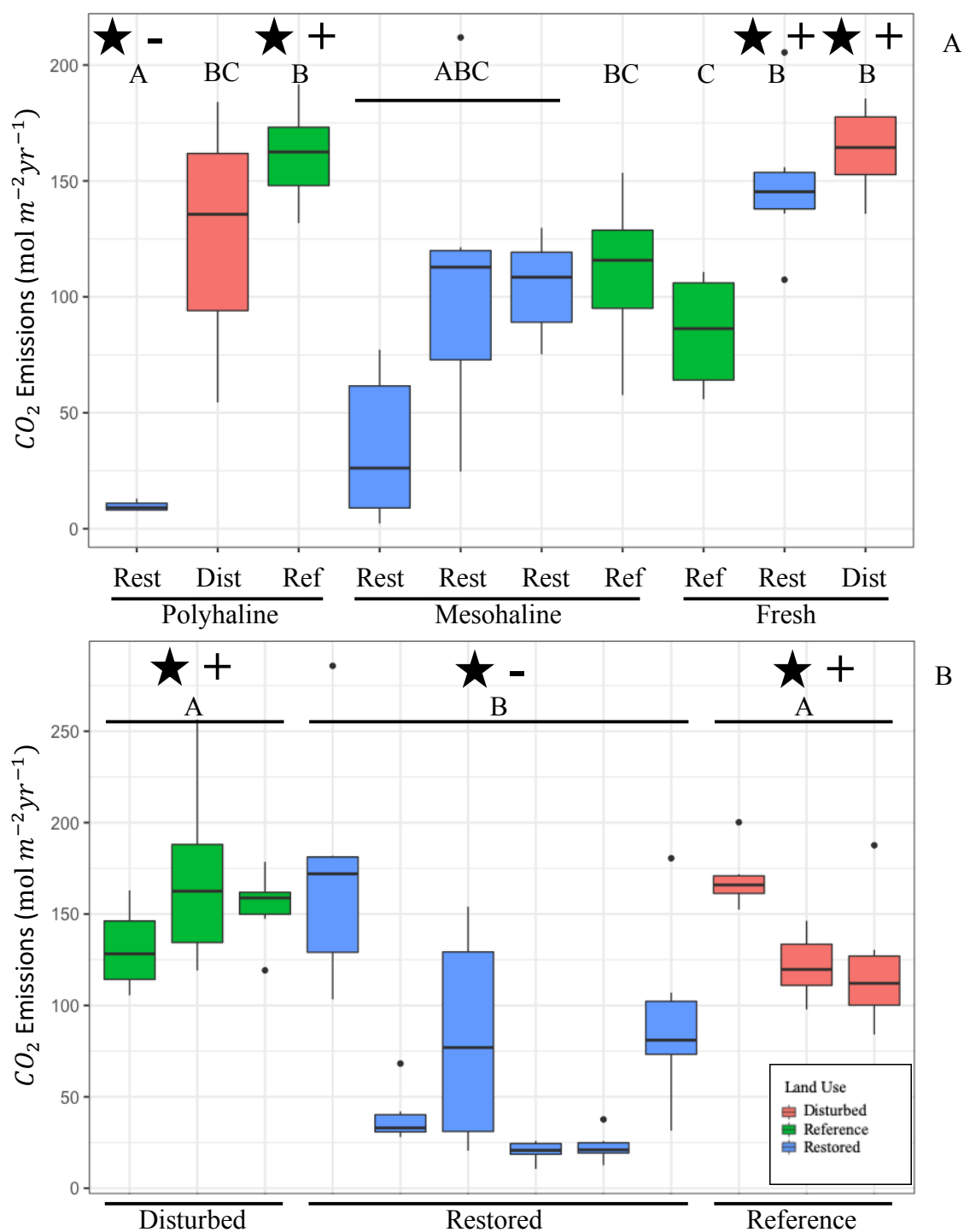


Figure 4. A. Annual CO_2 emissions in Coos Bay interpolated linearly between sampling dates. B. Annual CO_2 emissions in Tillamook Bay interpolated linearly between sampling dates. Red boxes represent disturbed sites, green boxes depict reference marshes, and red boxes represent restored marshes. Different letters indicate estimates of β whose 95% confidence intervals do not overlap and stars (+/-) indicate β estimates whose 95% confidence intervals are different from zero.

Dataset	Gas	Group	Mean	SD	2.50%	97.50%	Significance
Tillamook	CO2	Disturbed	0.21	0.09	0.04	0.38	*
		Reference	0.29	0.09	0.13	0.46	*
		Restored	-0.30	0.07	-0.43	-0.17	*
	CH4	Disturbed	-0.15	0.09	-0.33	0.02	
		Reference	-0.15	0.09	-0.32	0.02	
		Restored	0.18	0.07	0.05	0.31	*
	N2O	Disturbed	-0.02	0.09	-0.19	0.16	
		Reference	-0.29	0.09	-0.45	-0.12	*
		Restored	0.18	0.07	0.05	0.31	*
Coos Bay	CO2	Disturbed	0.32	0.13	0.06	0.57	*
		Reference	0.04	0.11	-0.17	0.25	
		Restored	-0.33	0.08	-0.48	-0.18	*
	CH4	Disturbed	-0.29	0.11	-0.51	-0.08	*
		Reference	-0.09	0.10	-0.28	0.10	
		Restored	-0.11	0.07	-0.25	0.03	
	N2O	Disturbed	0.02	0.08	-0.12	0.17	
		Reference	0.00	0.06	-0.11	0.11	
		Restored	0.01	0.07	-0.14	0.15	
Combined	CO2	Disturbed	0.27	0.07	0.14	0.41	*
		Reference	0.25	0.06	0.12	0.37	*
		Restored	-0.28	0.05	-0.38	-0.18	*
	CH4	Disturbed	-0.22	0.07	-0.36	-0.08	*
		Reference	0.02	0.06	-0.11	0.15	
		Restored	0.09	0.05	-0.01	0.19	
	N2O	Disturbed	0.08	0.07	-0.06	0.22	
		Reference	-0.26	0.06	-0.38	-0.13	*
		Restored	0.11	0.05	0.02	0.21	*

Table 2. Bayesian model β estimates for land use on observed GHG fluxes in Coos Bay, Tillamook, and combined datasets. Displayed are mean, standard deviation (SD), 95 % credibility intervals (2.5%; 97.5%), and significance (95 % credibility intervals different from zero).

ecosystem CO₂ emissions in Coos Bay and Tillamook Bay were in general agreement with the combined-site model, showing a primary effect of water-table height and air temperature (Supplemental Figure 3, Table 1). Bayesian models revealed no significant differences in methane emissions between high and low tides in Coos Bay (Supplemental Figure 4A).

Annual emissions in Coos Bay were lowest in the restored polyhaline marsh, and

the polyhaline reference and disturbed sites did not differ from each other (Figure 4A). Restoration e sites in Coos Bay had similar emissions. The reference freshwater wetland had lower annual emissions than the freshwater restored and disturbed sites. Both the freshwater restored and disturbed sites had net positive effects on annual emissions. Across the salinity gradient in Coos Bay, annual emissions were negatively influenced by restoration and positively influenced by disturbance (Supplemental Table 1). Annual CO₂ emissions in Tillamook were lower in the restored sites than the reference and disturbed sites, and the reference and disturbed land uses had a positive effect on emissions whereas restoration had a negative effect on emissions (Figure 4B, Supplemental Table 2).

B. Methane

Combined Sites. The CART model explained 21 % of the variation in CH₄ emissions. High salinity (> 3.5 ppt) yielded small CH₄ fluxes (mean = 1.0 mmol⁻² d⁻¹), while emissions were greatest when the salinity was less than 3.5 ppt, percent soil carbon greater than 9.93 %, and soil temperature greater than 15 ° C (mean = 31.8 mmol⁻² d⁻¹, Figure 5). Lower CH₄ emissions occurred in this group of sites at temperatures less than 15 °C (mean = 8.1 mmol m⁻² d⁻¹). Relatively high CH₄ emissions occurred in low salinity, disturbed, less organic sites when the water table was above – 1.5 cm (mean = 19.0 mmol⁻² d⁻¹). Lower emissions occurred in these sites when the water table was below – 1.5 cm (mean = 2.2 m mol⁻² d⁻¹). The lowest emissions occurred in low salinity, less organic, restored sites (mean = 0.3 mmol m⁻² d⁻¹). Random forest models (R² = 0.21) ranked the variables differently than the best CART, with soil and air temperature being the two most important variables, followed by water table, salinity, and pH (Table 1).

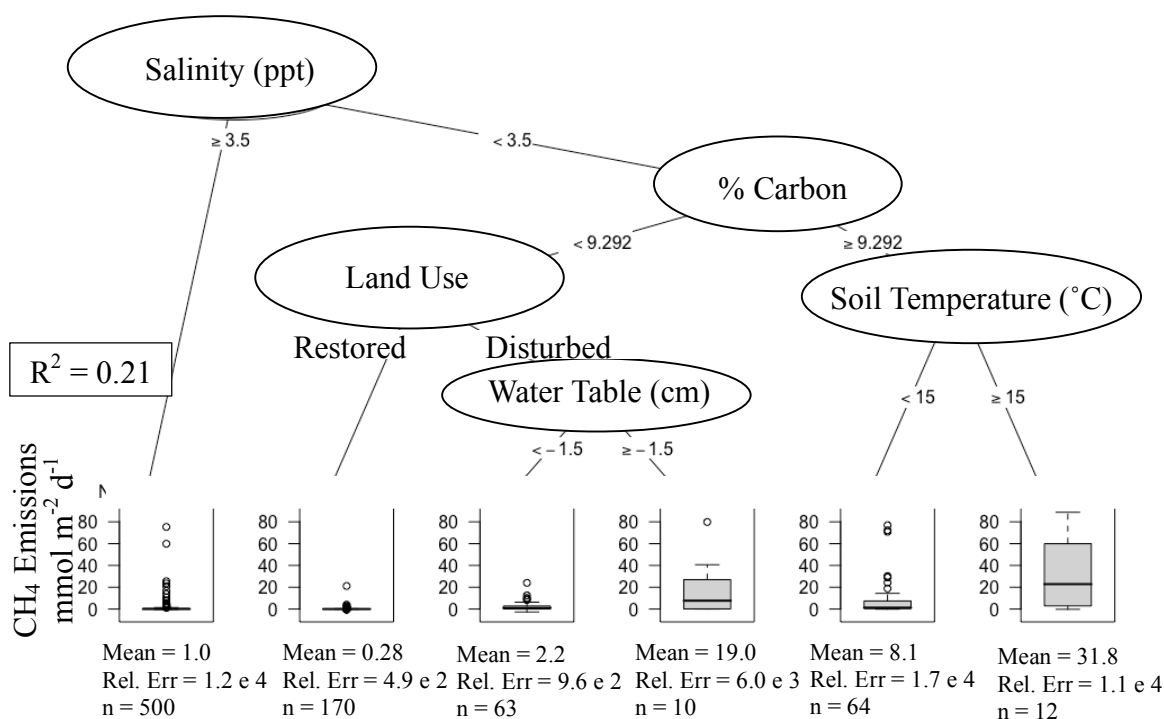


Figure 5. Summary of CART results for CH_4 emissions in PNW dataset. Ovals depict model splits with associated P-values. They correspond to terminal leaf boxplots with mean CH_4 emissions, relative error, and number of samples (n). The overall model Psuedo – $R^2 = 0.21$.

Individual environmental variables did not explain much of the variation in emissions in a straight forward linear manner (Supplemental Figure 5). Methane emissions and salinity were not highly correlated ($R^2 = 0.016$, $p < 0.001$, Supplemental Figure 5A), although it displayed a distinct cutoff around 18 ppt, after which CH_4 emissions were very low. The reference sites also tended to have lower water table levels because they were all high marshes. Bayesian models revealed that the disturbance negatively affected CH_4 fluxes and was different from the restored land use (Table 1).

Coos Bay and Tillamook Bay. CARTs for methane emissions in Coos Bay and Tillamook Bay showed a different hierarchy of controlling variables than when combined

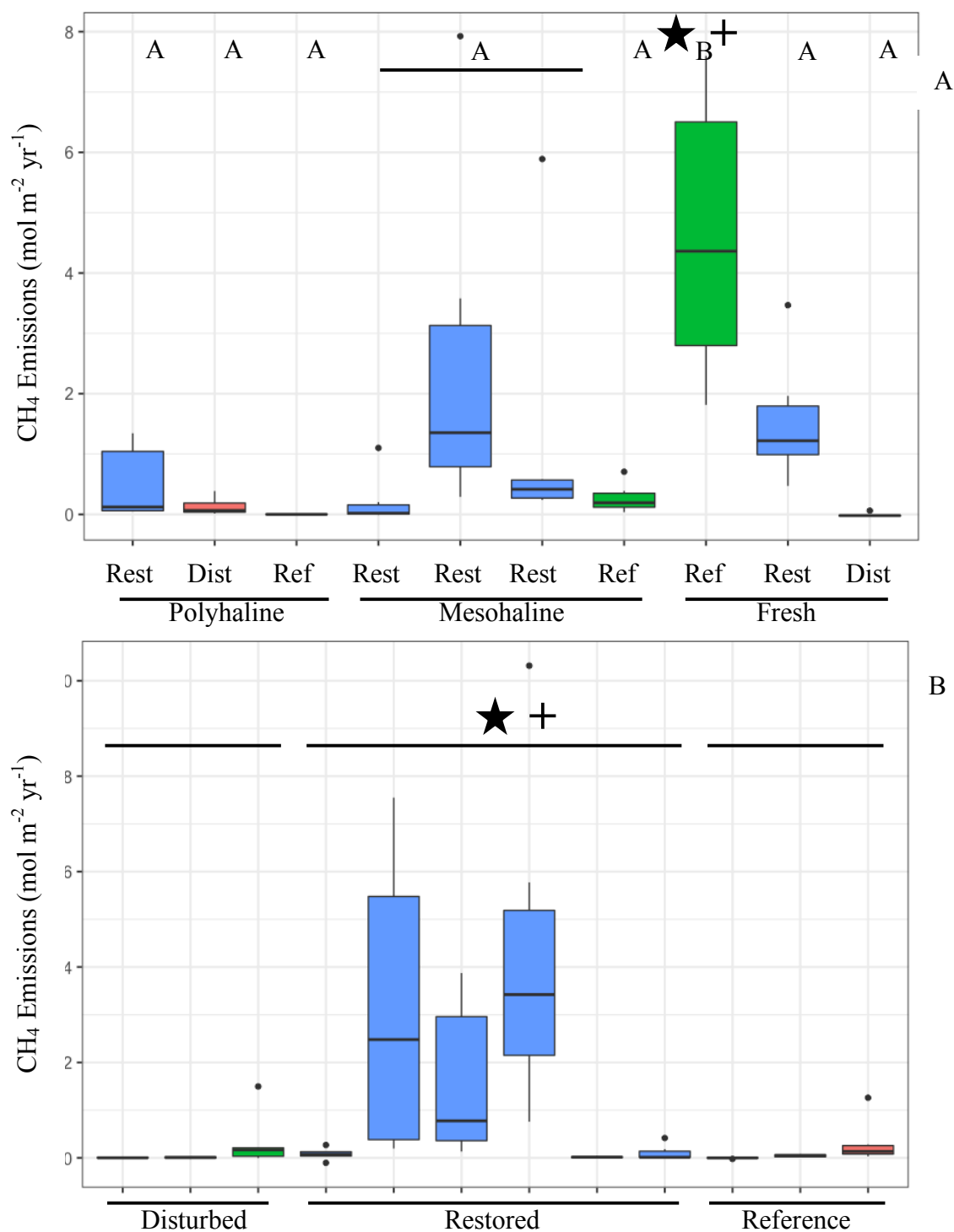


Figure 6. A. Annual CH_4 emissions in Coos Bay interpolated linearly between sampling dates. B. Annual CH_4 emissions in Tillamook Bay interpolated linearly between sampling dates. Red boxes represent disturbed sites, green boxes depict reference marshes, and red boxes represent restored marshes. Significance values were determined based on Bayesian models. Letters indicate estimates of β whose 95% confidence intervals do not overlap with each other and a star (+/-) indicate β estimates whose 95% confidence intervals are different from zero.

% soil carbon and secondarily by salinity, whereas Tillamook Bay was heavily influenced by water-table height, salinity and soil temperature. Random forests gave fairly different hierarchies of controlling variables in the two bays than the CARTs, although they were also not highly predictive ($R^2 = 0.10$ in Coos Bay and 0.21 in Tillamook Bay). Temperature was the most important predictor in Coos Bay, followed by % soil carbon and pH, and then salinity. In Tillamook Bay, water table and temperature were most important, followed by pH and salinity. Bayesian models revealed no significant differences in methane emissions between high and low tides in Coos Bay (Supplemental Figure 4B). The seasonal peak emissions varied among sites and treatments, but a sharp increase in emissions in the restored sites in Tillamook Bay in April and May was apparent (Supplemental Fig. 5).

Annual CH₄ emissions in Coos Bay were highest in the reference freshwater site (Figure 6A). Additionally, the disturbed land use had lower annual CH₄ emissions than reference and restored land uses (Supplemental Table 1). Furthermore, observed CH₄ fluxes were not statistically different between land uses (Table 1). In Tillamook, annual emissions and observed fluxes were greatest in the restored land use and restoration had a positive effect on emissions (Figure 6B, Supplemental Table 1, Table 1).

C. Nitrous Oxide

Combined Sites. Nitrous oxide emissions were sporadic, often below detection and included both positive and negative fluxes. In the CART, emissions were primarily controlled by pH, land use, and soil temperature, but the model only explained 12 % of the variation (Figure 7). Emissions were greatest when the pH was less than 5.1 (mean = $0.55 \mu\text{mol}^{-2} \text{d}^{-1}$). At higher pH, restored and disturbed sites had greater emissions than

reference sites, and within restored and disturbed sites, greater emissions occurred with warmer temperatures and lower pH. Random forests only explained 3 % of the variation of N_2O emissions and primarily controlled by pH (Supplemental Table 1). Observed fluxes in the restored sites were higher than in disturbed sites (Table 1). Restoration had a positive effect on N_2O emissions, whereas the reference land use had a negative effect.

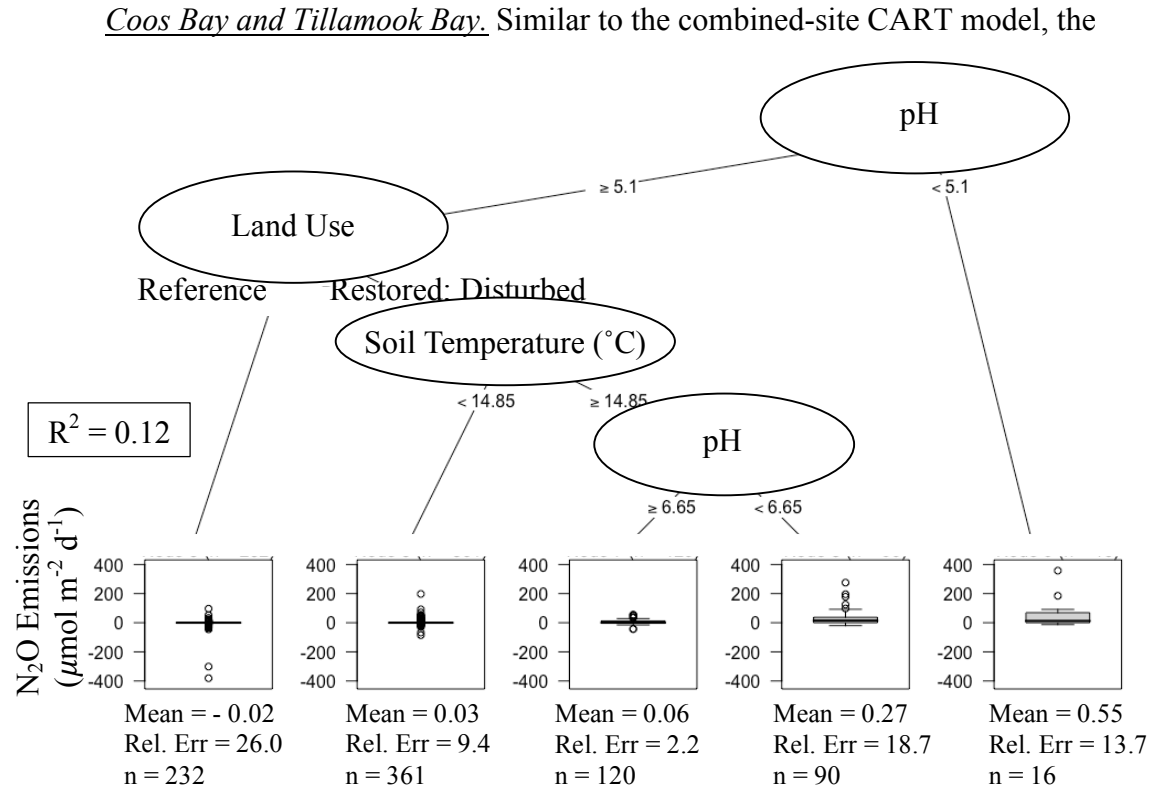


Figure 7. Summary of CART results for N_2O emissions in PNW dataset. Ovals depict model splits with associated P-values. They correspond to terminal leaf boxplots with mean N_2O emissions, relative error, and number of samples (n). The overall model Psuedo – $R^2 = 0.12$.

Coos Bay CART model predicted higher N_2O emissions at lower pH ($R^2 = 0.13$). It also predicted higher emissions in less organic soils (% soil carbon $< 8.1\%$) Random forests only explained 1 % percent of the variation of N_2O emissions in Coos Bay. The CART in

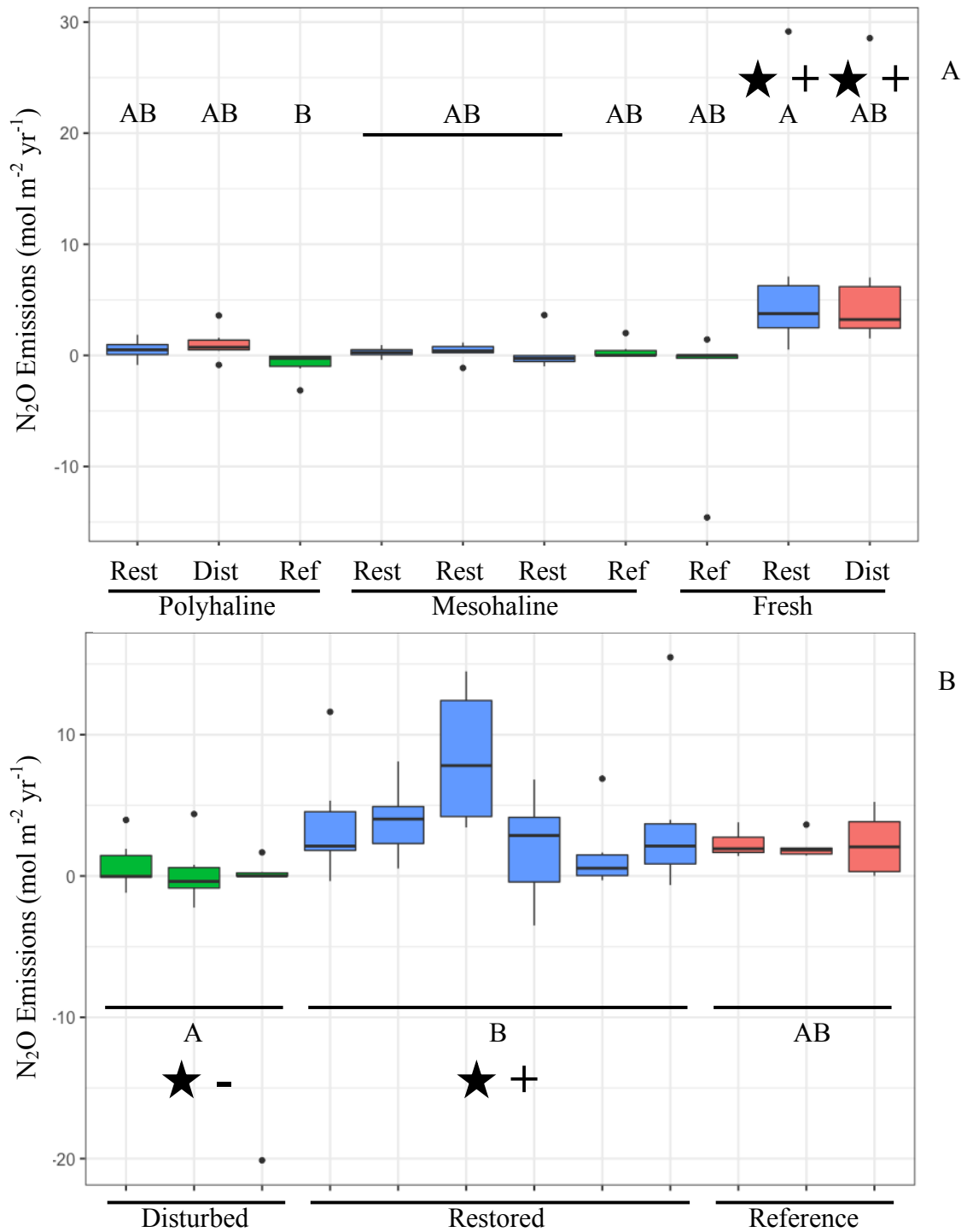


Figure 8. A. Annual N₂O emissions in Coos Bay interpolated linearly between sampling dates. B. Annual N₂O emissions in Tillamook Bay interpolated linearly between sampling dates. Red boxes represent disturbed sites, green boxes depict reference marshes, and red boxes represent restored marshes. Significance values were determined based on Bayesian models. Letters indicate estimates of β whose 95% confidence intervals do not overlap with each other and a star (+/-) indicate β estimates whose 95% confidence intervals are different from zero.

Emissions primarily controlled by soil temperature, air temperature, water table, and land use. Bayesian models showed no significant differences in N₂O emissions between high and low tide in Coos Bay (Supplemental Figure 4C). Random forest explained only 4 % percent of the variation of N₂O emissions in Tillamook ($p = 0.001$) and emissions were most notably influenced by soil temperature, air temperature, pH, and % carbon (Supplemental Table 1). None of the environmental predictor variables were highly correlated with N₂O emissions (Supplemental Figure 8).

Annual N₂O emissions in the restored fresh sites were statistically different from the reference polyhaline marsh, although this was the only difference between sites in Coos Bay (Figure 8A). Annual emissions of N₂O in Tillamook were highest in the restored and lowest in the reference sites. The effect of the disturbed land use was not statistically significant. Additionally, the observed fluxes were greater in the restored than the reference land use.

Discussion

Coastal wetlands sequester carbon at high rates, but the positive climatic benefits of this can be offset by their emissions of the potent greenhouse gases CH₄ and N₂O (Reddy and DeLaune 2008; Chapin and others 2011). There is great interest in quantifying these emissions to determine the potential benefits of restoration and the possibility for carbon credits (Windham-MyersLisamarie and Cai 2018). In this study, we analyzed GHG emissions in order to understand the physicochemical controls of GHG fluxes and how land use influences emissions. In general, while there were important differences in emissions by land use, these could be explained by the effect of land use on the physicochemical drivers.

Carbon Dioxide

Dark CO₂ emissions characterize ecosystem respiration, which includes heterotrophic and plant respiration. Ecosystem respiration was positively influenced by lower water tables and warmer temperature throughout all locations, which is widely consistent with known controls of plant and microbial respiration (Reddy and DeLaune 2008; Chapin and others 2011). Restored sites overall had lower CO₂ fluxes than disturbed and reference sites. In Coos Bay, this was largely driven by lower respiration in the sparsely vegetated restored mesohaline and polyhaline mudflats, but the Tillamook Bay restored sites had heavy cover of vascular vegetation but also generally had low respiration. The restored sites were all high marshes and had lower water table heights than most of the restored sites with their legacies of soil subsidence (Supplemental Figure 5B), likely reducing soil respiration. One consequence of higher water tables is greater methane emissions, and hence lower production of CO₂, when salinity is low (see discussion below) (Reddy and DeLaune 2008). Interestingly, restoration continued to have a negative effect on ecosystem respiration even after the effects of water table and temperature were accounted for in the combined site CART (Figure 3). Similar studies have found restoration to reduce CO₂ emissions in salt marshes (Adams and others 2012).

Methane

While their relative importance changed across the different analyses, CH₄ emissions were consistently controlled by a combination of water-table, salinity, % soil carbon, and soil temperature, which is supported by known controls of CH₄ emissions (Reddy and DeLaune 2008). In the CARTs, a salinity > 3.5 ppt was necessary for maximum emissions (Figure 5), and only low methane emissions occurred when

porewater salinity was > 18 ppt (Figure 9), which is remarkably consistent with cut offs in the literature (Poffenbarger and others 2011; Windham-MyersLisamarie and Cai 2018). When sulfate is available, methanogens are outcompeted by sulfate-reducing bacteria, thus inhibiting methanogenesis (Reddy and DeLaune 2008; Chapin and others 2011). Sea water has high sulfate concentration and is often a good surrogate for salinity. Our snapshot analysis of soil pore water sulfate concentration confirmed its correlation with salinity ($R^2 = 0.80$, $p > 0.001$).

Soil temperature was an important regulator of CH_4 emissions, and higher emissions occurred in the spring and summer (Supplemental Figure 4). Besides the direct positive effect of temperature on methanogenesis, organic matter decomposition and overall microbial activity is positively correlated with temperature (Reddy and DeLaune 2008), which would provide the methanogens with greater substrate supply. Water-table height is a well-documented control over methane emissions with a higher water table providing a greater anaerobic zone for the production of methane and a reduced zone for methane oxidation (Reddy and DeLaune 2008). However, water-table height played a much larger role in Tillamook Bay than Coos Bay and that is most likely due to the fact that the many of the sites in Tillamook were recently restored and have not gained enough surface elevation to reduce inundation. Additionally, the restored polyhaline site and the low, mesohaline restored cell in Coos Bay were largely mudflats and had low methane emissions despite being quite wet, probably because vascular plants providing substrates for methanogens (Whiting and Chanton 1993; Updegraff and others 2001). The primary effect of soil carbon percentage on methane emissions in Coos Bay reflects high emissions in the organic soils of the reference freshwater site.

The disturbed sites had low methane emissions because of the aerobic environment created by diking and draining of the wetland. All of the disturbed sites other than the freshwater site in Coos Bay regularly had high water tables during the winter rainy season, they still had relatively low instantaneous and annual methane emissions, probably because of cooler temperatures (even in the mild coastal climate of Oregon) and possibly because of oxidized terminal electron acceptors. Somewhat surprisingly, the disturbed polyhaline site had low methane emissions despite being relatively freshwater throughout most of it and dominated by wetland vegetation. If former salt marshes had high methane emissions, then restoration of them to a saline condition would have the added benefit of reducing methane emissions in addition to increasing soil carbon sequestration (Blount 2017), but this would require wetter conditions than in our research site to achieve the full greenhouse forcing benefit from restoration.

The effect of land use is somewhat muddled in Coos Bay, as the sites occur along a salinity gradient and are not replicates of each other, and we did not have a mesohaline disturbed site to complete the comparison. In Coos Bay, annual emissions were not statistically different for all except the reference fresh site, which produced the most CH₄. This is to be expected, as it has high soil carbon, high water table, and is a fresh water site. Wasson Creek is also a fresh water site, but it emitted low levels of CH₄, due to drainage and alteration of its water table. The restored fresh site produced intermediate CH₄ emissions. This could be due to the high levels of soil carbon in the reference site compared to the restored site (Reddy and DeLaune 2008). Mesohaline marshes can emit large fluxes of CH₄ (Poffenbarger and others 2011), but we report modest emissions,

which is likely due to large fluctuations in salinity and water table. Some high CH₄ emissions in the Kunz mid marsh could be explained by more frequent inundation patterns than the high marsh and halophytic dominated marshes produce more CH₄ than mudflats (Reddy and DeLaune 2008). The polysaline marshes emitted low levels of CH₄, which is expected due to the high sulfate concentration (Reddy and DeLaune 2008; Poffenbarger and others 2011; Adams and others 2012; Wollenberg and others 2018).

In Tillamook Bay, restoration resulted in increased CH₄ fluxes in some of the sites in the large restoration across a salinity gradient (Figure 6B). As described above, the disturbed Tillamook Bay sites, which were in active pasture management, had low methane emissions, so the short-term effect of restoration was to substantially increase methane emissions on average across the site. This recent restoration still suffered from the legacy of soil subsidence from its long history of disturbance, and thus some of the restored sites had a consistency high water table compared to the mature high marsh reference sites. This hydrology in connection with periods of low salinity during high river flows, reducing sulfate concentration, allowed for high methane emissions. We expect that over time as the restored marsh accretes sediments and moves higher in the tidal frame for methane emissions to decrease to levels closer to the reference sites. There is also an unknown effect of the very different plant communities between the restored sites and the reference sites, and we expect the communities of the restored sites to more closely resemble those of the reference sites over time.

Nitrous Oxide

Nitrous oxide emissions were low, episodic, and could be positive or negative. Given this, all models explained very little of the variation. Soil temperature and pH had

the largest effect on emissions and are known regulators of denitrification and nitrification, the two major producers of nitrous oxide (Reddy and DeLaune 2008). Other studies have found that wetlands have low nitrous oxide emissions unless they have major nitrogen inputs (find references for this statement). This is important because nitrous oxide has 263 times the sustained-flux global warming potential as CO₂ over a 100-year timeline (Neubauer and Megonigal 2015). Overall, emissions were highest in restored sites and lowest in reference sites, inferring that sites may become small sources of N₂O following restoration (Adams and others 2012; Wollenberg and others 2018). This trend was apparent in Tillamook, where agricultural runoff from upstream farm fields could promote N₂O emissions (Nirmal Rajkumar and others 2008). Additionally, emissions in restored sites peaked in the summer across both sites, which is consistent with Harley and others (2015).

CHAPTER III

CONCLUSION

Dark chamber CO₂ emissions were heavily influenced by water table height and temperature, while CH₄ emissions were primarily controlled by salinity, % soil carbon, and water table. Together, the height of the water-table played a large role in emissions and should be a primary consideration when restoring tidal marshes. Restoring coastal wetlands may present climactic trade-offs, where high carbon sequestration rates (Reddy and DeLaune 2008) may initially be offset by CH₄ emissions, but as the marsh accumulates sediment, the water table will lower, producing less CH₄.

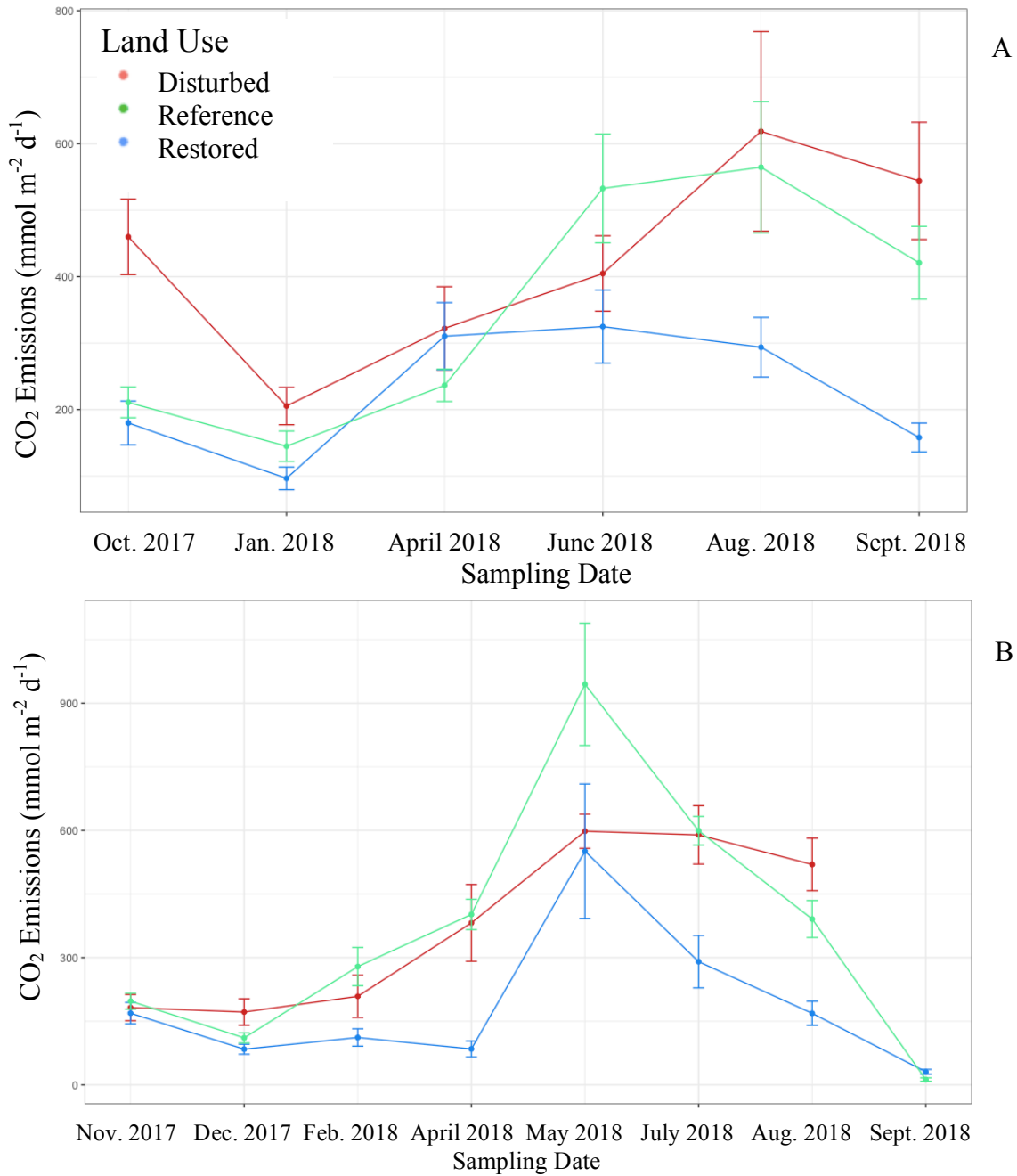
Nitrous oxide emissions were heavily influenced by pH, which is supported by the literature (Reddy and DeLaune 2008), although the sporadic nature of the measurements led to low model correlation. Restoration did have a positive effect on emissions. Together, increased CH₄ and N₂O emissions in restored coastal wetlands could offset their high carbon sequestration rates, due to their high sustained global warming potential (Neubauer and Megonigal 2015).

Due to the heterogenous sites and their complex differences in salinity, vegetation, water-table level, physicochemical variables, and land-use, much less variation was explained in both single regressions and in the CARTs than is often the case in the literature. The effect of land use was sometimes large and significant, but it could largely be explained by the effects of land use on ecosystem drivers. While more sampling points and sites is always desirable, we do not expect the predictability of methane emissions to increase substantially with additional data. This will provide a substantial management limitation in the planning wetland restorations to minimize GHG

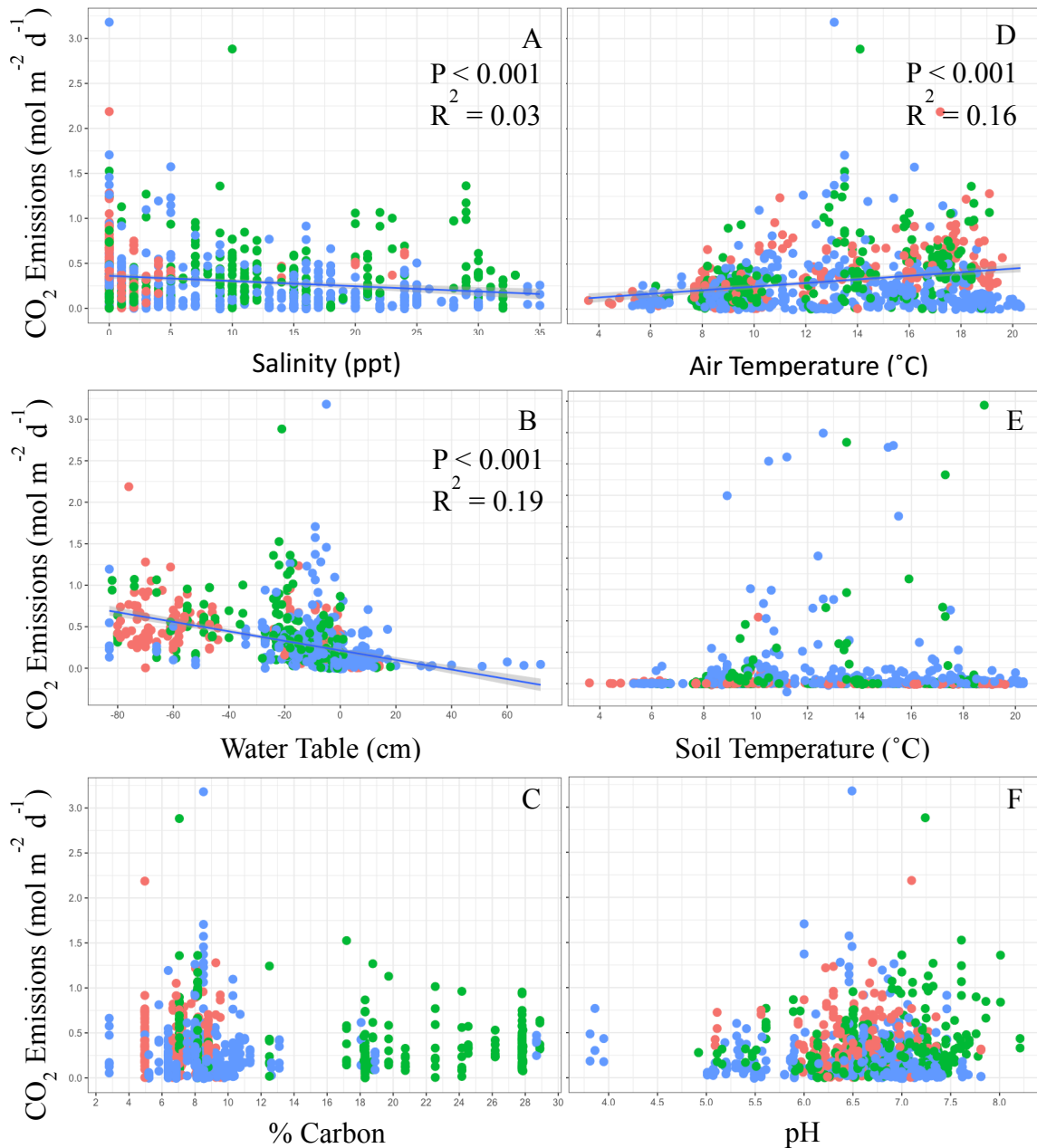
emissions.

Carbon cycling is just one of the many ecosystem services that coastal wetlands provide (Chapin and others 2011; Dahl and Stedman 2013; Mitsch and Gosselink 2015). While it may take time to recover the carbon cycling benefits associated with coastal wetlands, communities such as Tillamook may receive immediate relief in flood control. In order to determine whether these sites are net sources or sinks, a full carbon budget should be completed. We are analyzing carbon sequestration rates and compiling a complete carbon budget for both of these estuaries. Estuaries in Oregon have shown resilience, with sedimentation rates (Thorne and others 2018) exceeding the current rate of sea level rise (Komar and others 2011), inferring that they will continue to persist and acquire carbon for the foreseeable future.

APPENDIX: SUPPLEMENTAL FIGURES AND TABLES

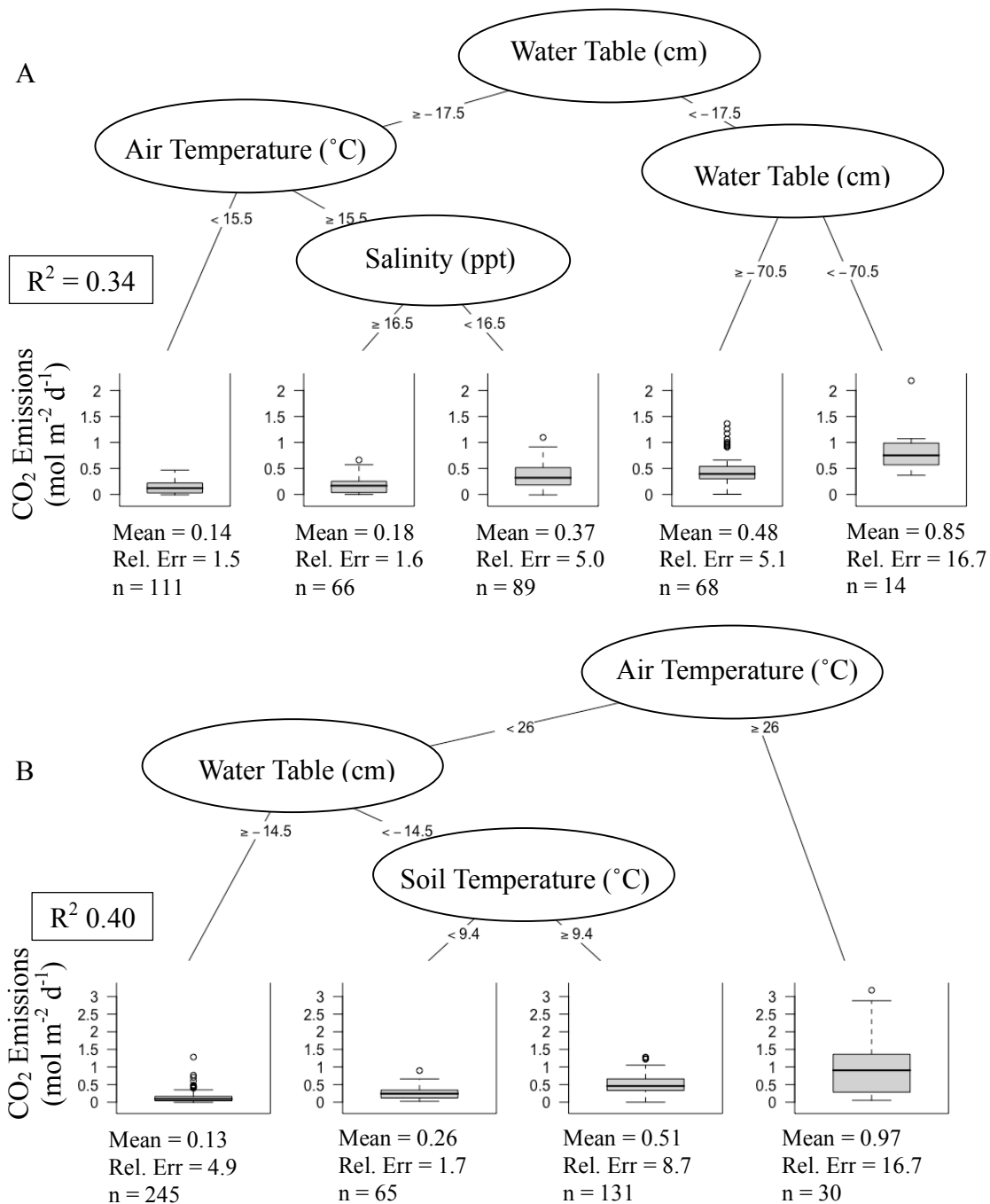


Supplemental Figure 1. Observed CO₂ emissions in Coos Bay (A) and Tillamook (B) over one water year.

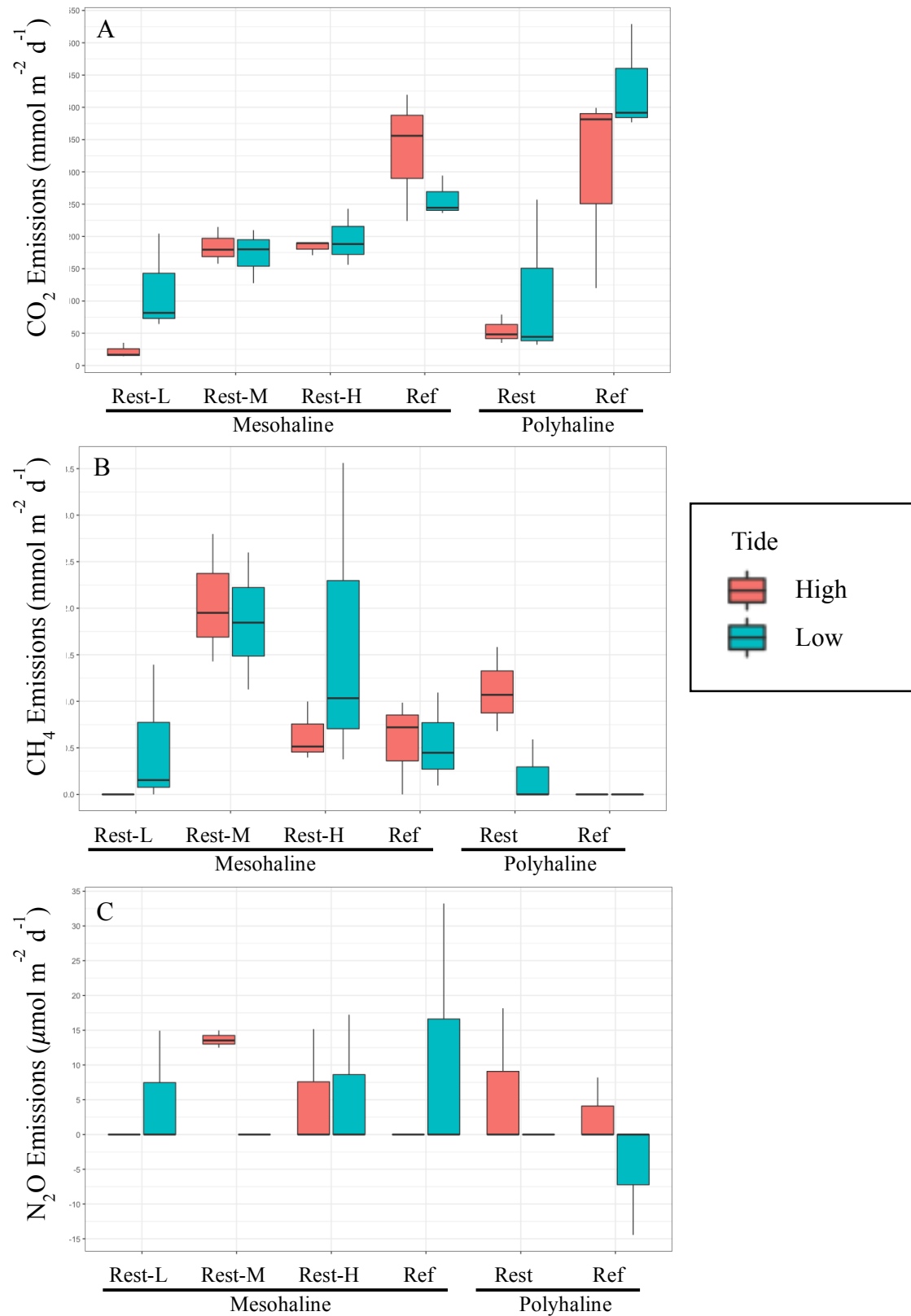


Supplemental Figure 2. Scatterplot of observed dark chamber CO₂ fluxes against environmental variables for the combined dataset. When the regression was significant, the blue line depicts the linear trendline with gray 95% confidence intervals with associated P-value (P) and correlation coefficient (R²).

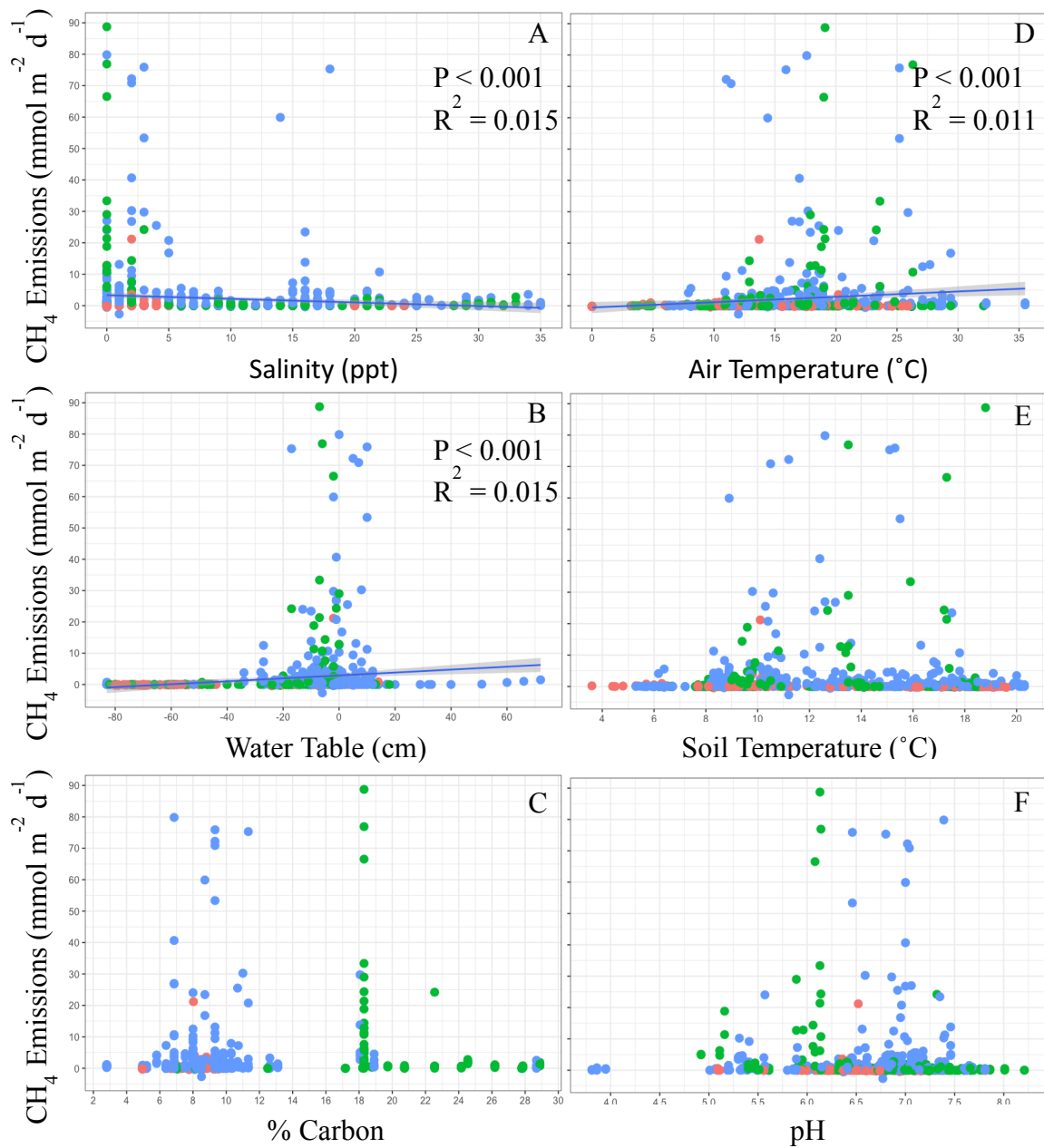
Land Use
 • Disturbed
 • Reference
 • Restored



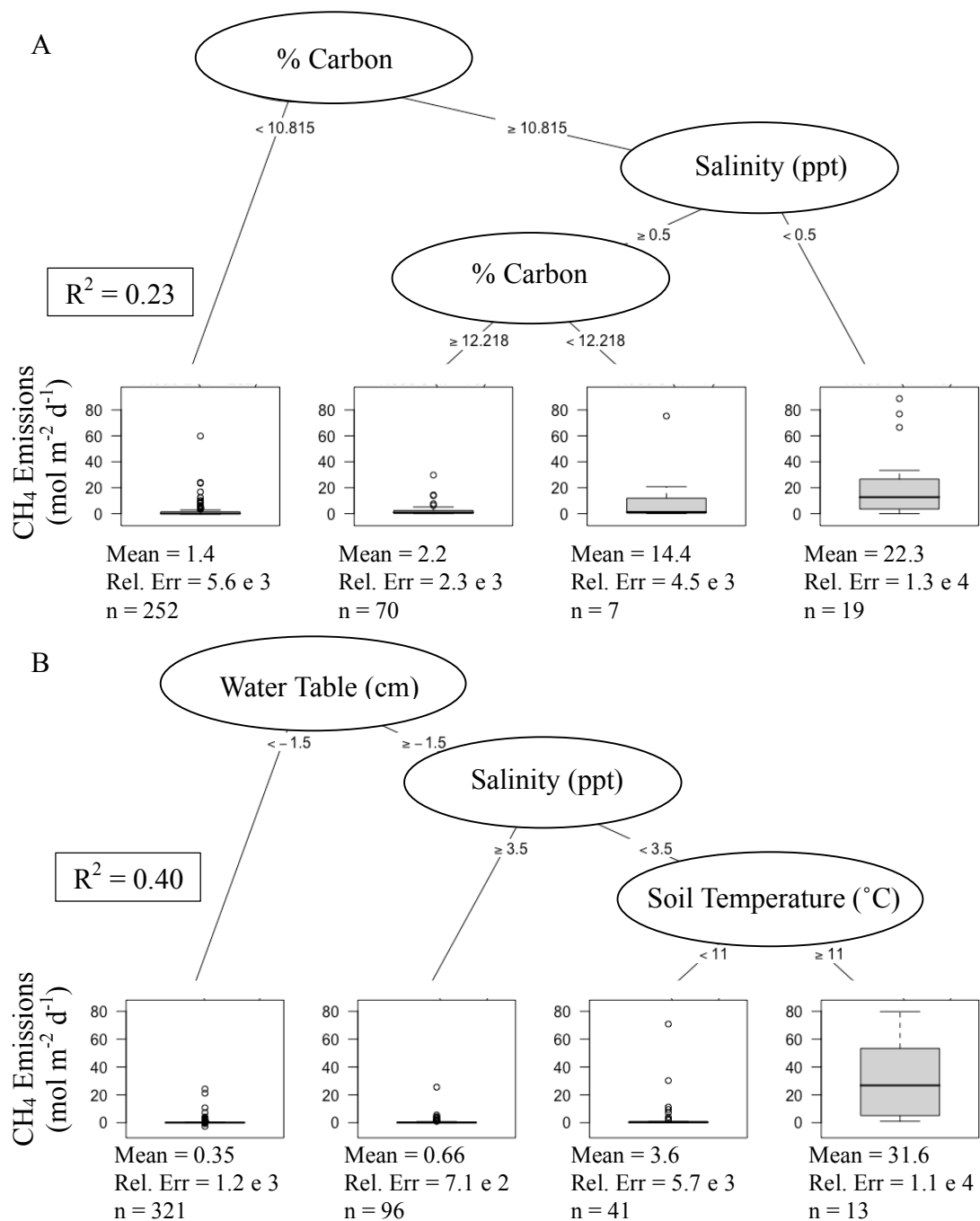
Supplemental Figure 3. Summary of CART results for CO₂ emissions in Coos Bay (A) and Tillamook Bay (B). Ovals depict model splits with associated P-values. They correspond to terminal leaf boxplots with mean CO₂ emissions, relative error, and number of samples (n). The overall Coos Bay model Psuedo – $R^2 = 0.34$ and Tillamook model Psuedo – $R^2 = 0.40$.



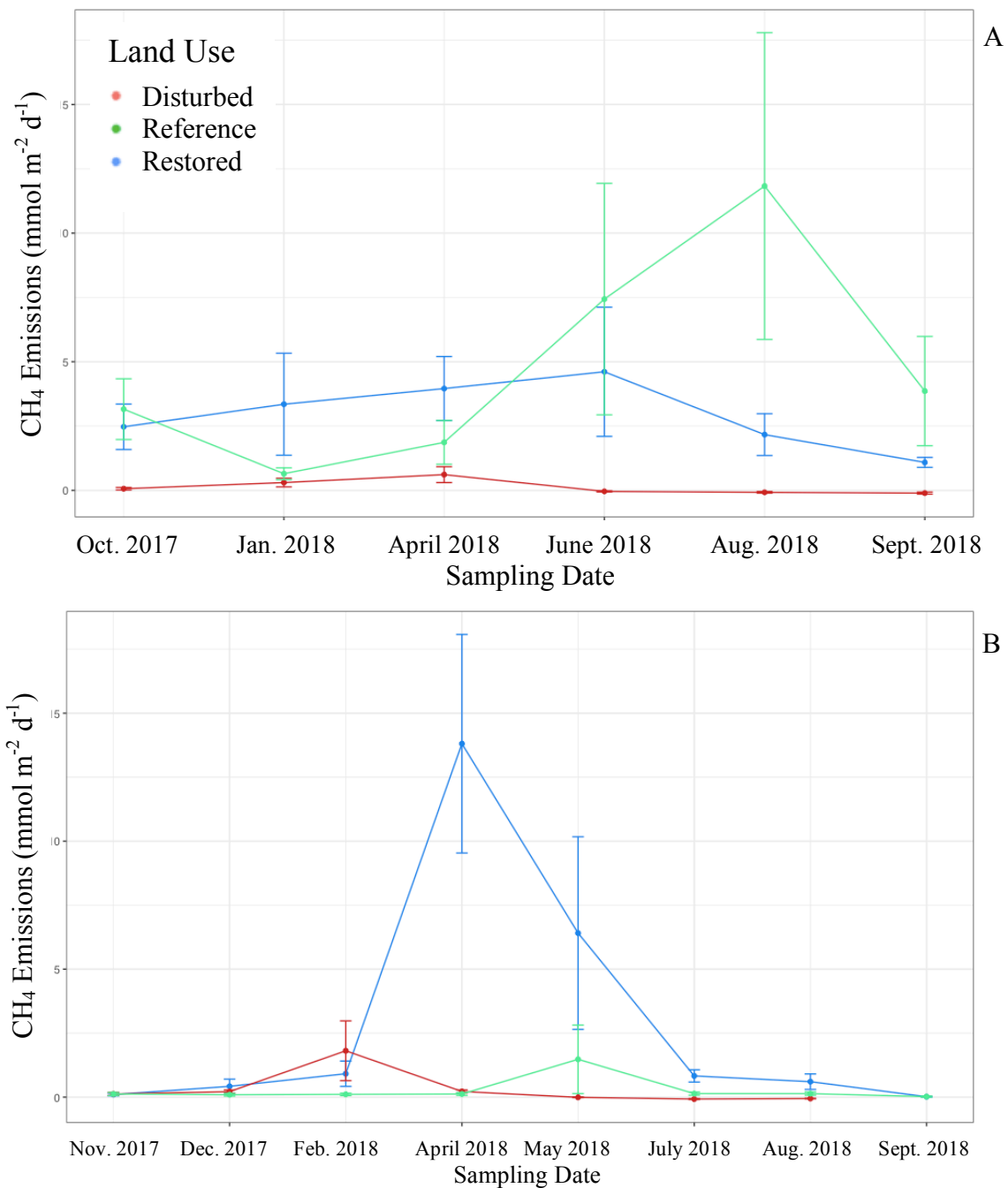
Supplemental Figure 4. High tide sampling of GHG emissions in Coos Bay. A. Carbon dioxide. B. Methane. C. Nitrous oxide.



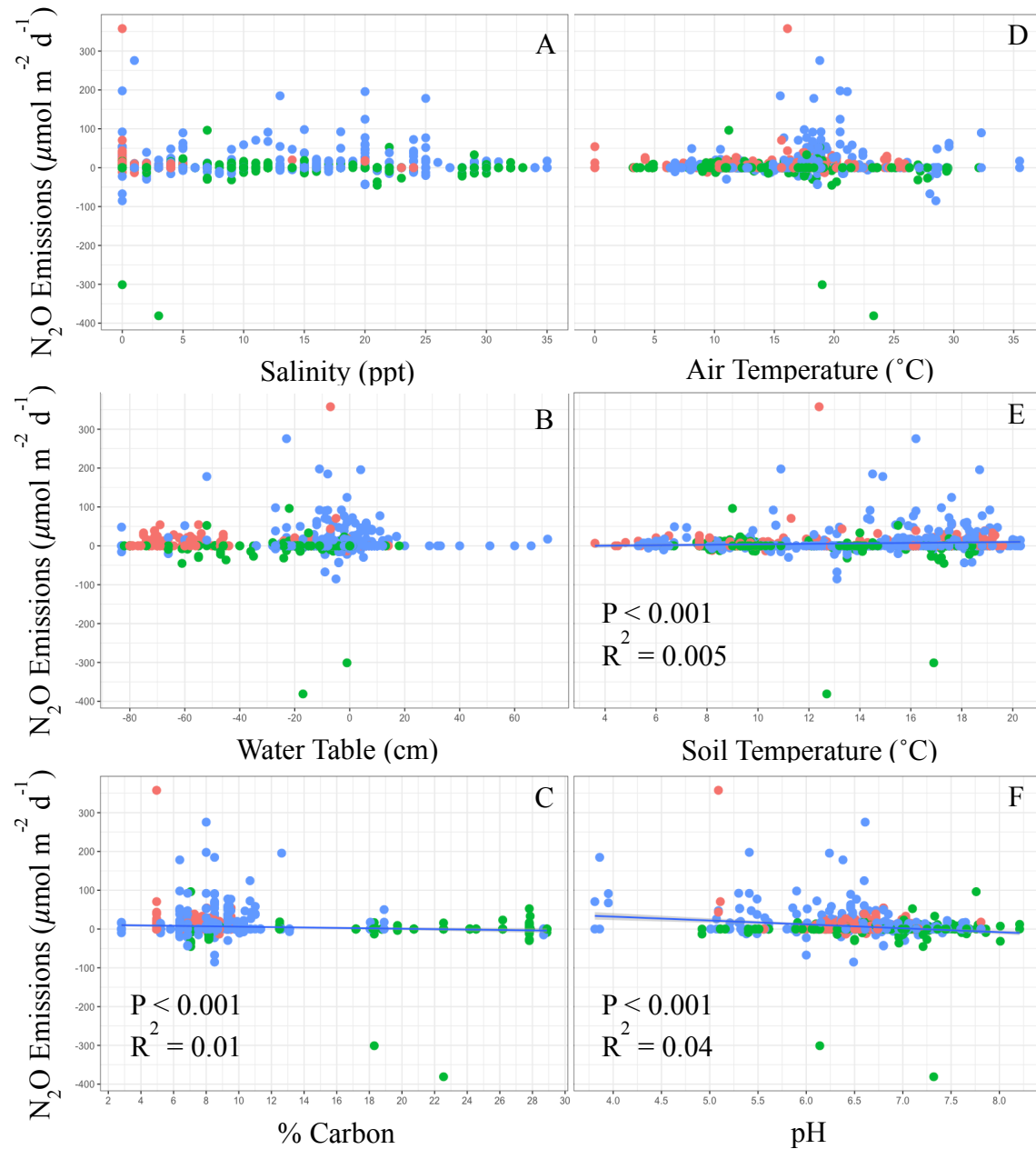
Supplemental Figure 5. Scatterplot of observed CH₄ fluxes against environmental variables for the combined dataset. The blue line depicts linear trendline with gray 95% confidence intervals with associated P-value (P) and correlation coefficient (R²).



Supplemental Figure 6. Summary of CART results for CH_4 emissions in Coos Bay (A) and Tillamook Bay (B). Ovals depict model splits with associated P-values. They correspond to terminal leaf boxplots with mean CH_4 emissions, relative error, and number of samples (n). The overall Coos Bay model Psuedo – $R^2 = 0.23$ and Tillamook model Psuedo – $R^2 = 0.40$.



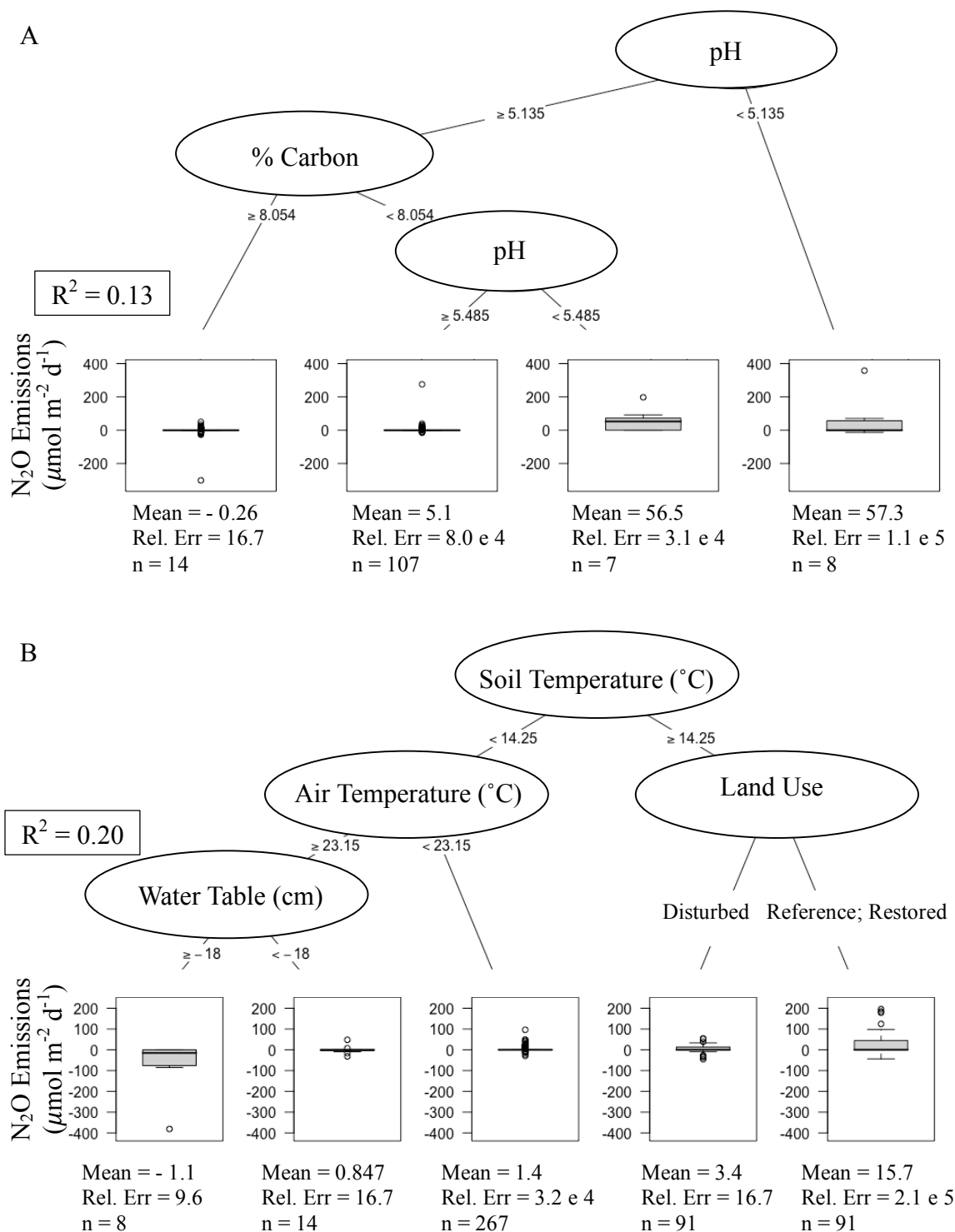
Supplemental Figure 7. Observed CH₄ emissions in Coos Bay (A) and Tillamook (B) over one water year.



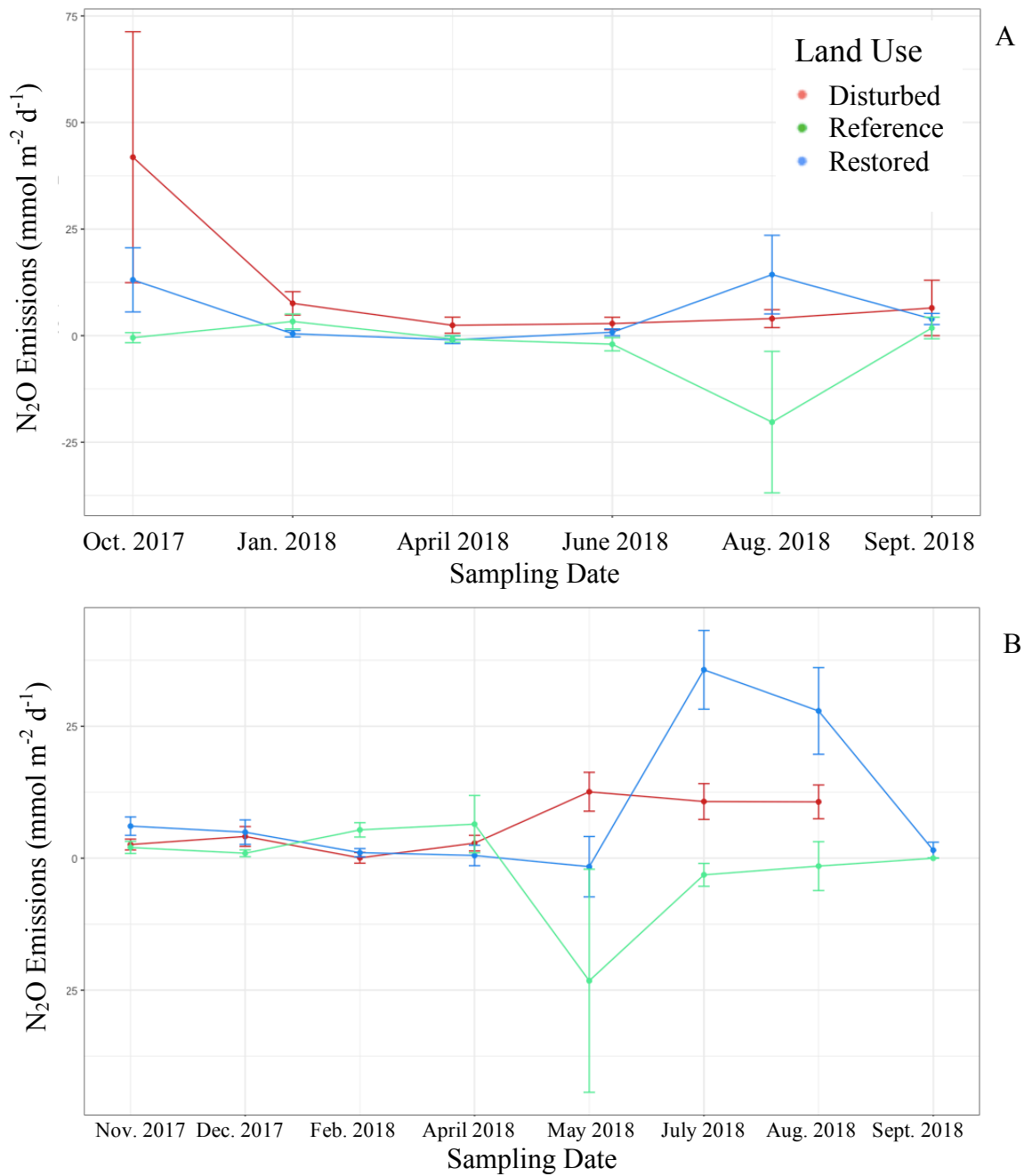
Supplemental Figure 8. Scatterplot of observed N_2O fluxes against environmental variables for the combined dataset. The blue line depicts linear trendline with gray 95% confidence intervals with associated P-value (P) and correlation coefficient (R^2).

Land Use

- Disturbed
- Reference
- Restored



Supplemental Figure 9. Summary of CART results for N₂O emissions in Coos Bay (A) and Tillamook Bay (B). Ovals depict model splits with associated P-values. They correspond to terminal leaf boxplots with mean N₂O emissions, relative error, and number of samples (n). The overall Coos Bay model Psuedo – $R^2 = 0.13$ and Tillamook model Psuedo – $R^2 = 0.20$.



Supplemental Figure 10. Observed N₂O emissions in Coos Bay (A) and Tillamook (B) over one water year.

Dataset	Gas	Group	Mean	SD	2.50%	97.50%	Significance
Tillamook	CO ₂	Disturbed	0.46	0.20	0.06	0.85	*
		Reference	0.68	0.20	0.29	1.07	*
		Restored	-0.57	0.14	-0.85	-0.29	*
	CH ₄	Disturbed	-0.37	0.23	-0.82	0.07	
		Reference	-0.37	0.23	-0.82	0.08	
		Restored	0.37	0.16	0.05	0.69	*
	N ₂ O	Disturbed	-0.04	0.22	-0.47	0.39	
		Reference	-0.67	0.22	-1.12	-0.24	*
		Restored	0.35	0.16	0.04	0.66	*
Coos Bay	CO ₂	Disturbed	0.69	0.27	0.16	1.22	*
		Reference	0.24	0.22	-0.19	0.66	
		Restored	-0.42	0.17	-0.75	-0.08	*
	CH ₄	Disturbed	-0.54	0.26	-1.06	-0.02	*
		Reference	-0.08	0.27	-0.59	0.46	
		Restored	-0.11	0.18	-0.47	0.26	
	N ₂ O	Disturbed	0.49	0.29	-0.08	1.06	
		Reference	-0.42	0.23	-0.87	0.05	
		Restored	0.05	0.18	-0.31	0.41	

Supplemental Table 1. Bayesian model β estimates for land use on annual GHG emissions in Coos Bay and Tillamook. Displayed are mean, standard deviation (SD), 95 % credibility intervals (2.5%; 97.5%), and significance (95 % credibility intervals different from zero).

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